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The Cytology of Endochytrium operculatum (de Wildeman) Karling in Relation to its Development and Organization

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(WITH PLATES 1–7)

INTRODUCTION

As now recognized by most mycologists, the family Rhizidiaceae is the largest of the chytrid groups; it is reported to include 31 genera and about 198·species. Whether or not it constitutes a natural phylogenetic group or several separate families is at present uncertain. The family as a whole is characterized by a monocentric thallus which consists of an incipient zoosporangium or resting spore and an absorbing or rhizoidal system of varying complexity and size. In most cases resting spores are unknown or formed asexually similarily to the zoosporangia, but sexual reproduction has been reported in about 10 genera and 21 species, and exhibits great variability. Fusion of the protoplasts of equal and unequal thalli through pores, rhizoids, and conjugation tubes; fusion of motile isogametes, and a small female thallus with a motile male gamete or vice versa have been described in the literature. Accordingly, on the basis of variations in sexuality, few of the genera in this family seem to be closely related.

In spite of its size and significance in the phylogeny of the Chytridiales, and the wide variations in sexuality it exhibits, the family Rhizidiaceae has attracted very little attention from cytologists, and so far only three or possibly four species, *Polyphagus Euglenae*, *Zygorhizidium Willei*, *Sporophlyctis rostrata* and *Rhizophidium Beauchampi* have been studied from fixed and stained material.

The cytological problems presented by the Rhizidiaceae are numerous and varied. Before we can arrive at definite and final conclusions as to

the phylogeny and the relationships of the family, the cytology of the varied types of sexual reproduction, cell and nuclear fusions, meiosis, and their relations to the alternation of monoploid and diploid generations must be understood. So far it is not known whether the respective gametes are derived from the same or different thalli and gametangia, nor at what stage in the life cycle meiosis occurs, and little is known about the details of nuclear division, cleavage, sporogenesis, and the structure of the swarmspores in the group as a whole. One of the most baffling and interesting problems presented by this group is the cause of the constancy of the monocentric type of thallus. It has been suggested by Karling (1937b) that this is associated with, or perhaps determined by, the localization of the nuclei in the incipient zoosporangia and resting spores during the development of the thallus. A thorough study of the relation of nuclear distribution to the development of the thallus might thus throw some light on the causes of the characteristic monocentric type of organization in the Rhizidiaceae.

Endochytrium operculatum has been chosen for the study of some of the problems noted above because it is a typical, intramatrical representative of the Rhizidiaceae, and because of its large size, availability and abundance throughout the year. The identity and possible relationships of this species have been fully discussed by Karling (1937a) so that they need not be further considered here.

MATERIALS AND METHODS

Endochytrium operculatum grows intramatrically in cells of *Nitella* and *Cladophora*. The material used for this study was obtained at Columbia University by placing bleached and cooked filaments of these algae in greenhouse tanks previously infected with *Endochytrium*. These filaments were held in small cheesecloth or bobinet bags as employed by Karling (1935) in his study of *Cladochytrium replicatum*. Usually a heavy infection of *Endochytrium* occurred in six to ten days. The infected material was brought into the laboratory and washed in distilled water to remove bacteria and protozoa. It was then transferred to fresh spring water containing bleached and sterilized *Cladphora* filaments. About every ten days the cultures were washed and transferred to culture dishes containing fresh water and freshly prepared *Cladophora* filaments. In this way was maintained a stock culture of the fungus from which sub-cultures could be started. Sterile charcoal water was sometimes used instead of spring water, but it was found to check vegetative development and induce the formation of resting spores. In order to facilitate seeing the fungus

within, the *Nitella* filaments were first boiled in alcohol to remove the chlorophyl as done by Karling (1937a) in his studies of *E. operculatum.*

For observation of the living chytrid, *Cladophora* was found to be more convenient, since it may be kept dried in the laboratory for use at any time. The filaments of *Cladophora* growing out-of-doors are usually covered with such a growth of diatoms and other epiphytes that the intramatrical chytrid is obscured. To remove this overgrowth from the algal filaments, to soften the wall, and to make the protoplasm more homogeneous, the dried algae were boiled in 10% KOH for 15 minutes and then thoroughly washed in water. There seems to be little difference in the degree of infection between the material treated by hydroxide and the untreated material. Another method employed in removing the diatoms was to place the filaments in 15% hydrofluoric acid for three days, and then wash in water for several hours. Although in this case the *Cladophora* cells became heavily infected with *E. operculatum,* its subsequent rapid deterioration made such material unsuitable for study.

For sectioning and staining, infected internodes of *Nitella* were used exclusively, since the cell wall of *Cladophora* is difficult to section. A variety of fixatives was used: Allen and Wilson's modification of Bouin's, Merkel's, Carnoy's, absolute alcohol, chrom-acetic, Feulgen's, and Flemming's strong, medium, and weak solutions in various dilutions. Allen and Wilson's fixative in normal and one-half strength, Flemming's medium in one-fourth strength, and Flemming's weak solution diluted with distilled water to one-half strength were found to give the best results and were regularly employed. The other fixatives were used only for special purposes. Forty-eight hour fixing was found to give more satisfactory results than shorter periods.

Whole mounts, for the study of nuclear distribution in relation to organization, were prepared by fixing and washing *Cladophora* and *Nitella* in the usual manner, and then staining them *in toto* in vials with Heidenhain's iron-haematoxylin. The filaments were dehydrated and removed to a hanging-drop slide where they were counter-stained with alcoholic Orange G., rinsed with absolute alcohol, and cleared in xylol. Next, the material was placed in xylol on a slide, separated, and covered with balsam. Permanent mounts were also made in lacto-phenol containing a mixture of methyl blue and acid fuschin according to Maneval's formula (1936). This was a very satisfactory way of demonstrating the presence of nuclei in developing sporangia and resting spores.

Flemming's triple stain, Feulgen's, and Heidenhain's iron haematoxylin were relied upon for details of nuclear structure. Janus green

which is claimed to be specific for chondriosomes was used as an intra-vitam stain in dilutions of 1:100,000, 1:250,000, and 1:500,000.

To determine the composition of the large amount of highly refrac-tive substance found in all stages of development of the fungus, ether, xylol, chloroform, acetic acid, and the fat stains Sudan III and Scarlach R (Sudan IV), Nile blue sulfate, and osmic acid were used. In addition, two tests for glycogen were made: the iodine test with iodine-potassium iodide, and Best's carmine method, according to Galigher (1934). The cell walls were tested for cellulose with iodine-potassium iodide followed by sulfuric acid and zinc chloriodide, and for chitin by hydrolysis with potassium hydroxide to chitosan using the method described by Rawlins (1933).

Zoospores and their germination stages were studied from fixed and stained preparations. If germination stages were desired, the slide was smeared with a drop of agar and dried by being passed through a flame two or three times. *Cladophora* filaments containing sporangia about to discharge their zoospores were placed in a drop of distilled water on the slide and the slide placed in a moist chamber, until the zoospores had been discharged or germination had occurred. For fixation the slide was inverted over the mouth of a bottle containing 2% osmic acid for 30 seconds, dried, and passed twice through an alcohol flame to fix the zoospores or germination stages to the slide. The material was stained in acid fuchsin—cotton blue in lacto-phenol, either directly or after fixation for two hours in Allen and Wilson's or Flemming's weak solu-tion. The stain used was either Heidenhain's haematoxylin followed by alcoholic Orange G., or gentian violet after the method of Cotner (1930a).

OBSERVATIONS

Since the structure and development of *Endochytrium operculatum* (de Wildeman) Karling has been described from living material by de Wildeman (1895), Sparrow (1933), and Karling (1937a), it would be superfluous to repeat their observations. However, in order to compare the stages in living material with the corresponding stages in fixed and stained material, it will be necessary to deal briefly with the develop-mental stages in both.

Structure of the Zoospore

The living zoospore is hyaline, spherical to oval in shape, 3.9μ to 5.4μ in diameter with a single posterior cilium about five times as long as

the diameter of the zoospore body. The active swimming period of the zoospore varies from several minutes to a few hours, with occasional interruptions of quiescent and amoeboid periods during which the zoospores creep about on the substratum for a few seconds or minutes, then round up again and swim away. In exceptional cases, zoospores discharged into the host cell remain active for as long as six hours. The most prominent structure of the zoospore is the large, highly refractive globule, 1.57–2.4μ in diameter, whose position relative to the cilium does not appear to be fixed. It may lie in the anterior position, as in fig. 1, near the membrane at the side, as in fig. 2, or near the posterior end of the zoospore. Thus if the globule is oriented toward the cover slip, it may appear to occupy the center of the zoospore, as in fig. 3. The globule appears quite fluid and when the zoospore creeps through a tight place under the cover glass, the globule may undergo changes in shape as shown in figure 4. Its composition is apparently very complex, but it usually gives much the same reaction as oil. It is usually dissolved by xylol in the fixation and staining of material, leaving a more or less clear space in the cytoplasm at the anterior end of the zoospore as in figure 5, or in whatever region it occupied at the time of fixation. Figure 6 shows a fixed and stained zoospore with a lighter region in the anterior part of the nuclear cap which resembles the space left in the dissolution, of the refringent globule. If such is the case, it is obvious that the globule may sometimes lie in the substance which makes up this cap.

Closely associated with the refringent globule in the living material is another body of a rather indefinite outline and structure, which may be the nucleus and nuclear cap which are so conspicuous in fixed and stained material. In addition to these structures there may be a small granule which moves about in the cytoplasm and occasionally one or more granules in the cytoplasm as in figure 1.

The fixed and stained zoospore is quite different in appearance from the living zoospore. The refringent globule, as such, is no longer present, and the most conspicuous structure is the clear, spherical nucleus partly surrounded by a densely staining mass which constitutes the so-called extra-nuclear cap as is shown in figures 5 and 6. Since the nucleus is usually less than 2μ in diameter and is surrounded by such a large amount of extra-nuclear material it is difficult to see its internal structure. As is shown in figures 5–10, it is usually spherical in shape, comparatively transparent, and may be identified by the small, densely stainable, somewhat flattened, disc-shaped nucleolus. This structure is particularly evident near the zoospore wall in figure 10. As is shown in

this figure and in figure 7, a second densely stainable body may be present, but it appears to be outside of the nuclear membrane and constitutes a part of the nuclear cap. Besides the nucleole little can be seen, and I have been unable to observe a definite nuclear reticulum.

The nuclear cap stains deeply with haematoxylin, safranin and gentian violet but, like the nucleole, does not stand out very sharply in shape and color when fixed and stained by the Feulgen technique. It varies considerably in size and shape as figures 5–10 show. It may surmount the nucleus as a crescentic body as in figure 5, or almost completely surround it as in figure 6. Figures 5 and 6 were drawn from material fixed in Flemming's weak solution, sectioned, and stained by Heidenhain's iron-haematoxylin method, while figures 7–10 represent zoospores fixed *in toto* with osmic acid and stained directly in haematoxylin. The latter group did not stain as intensely as the former, nor is the nuclear cap as distinct. In figure 7 the nuclear cap is small and indistinct. These marked variations, although possibly due to the technique employed, or to variations in the relative amount of nuclear cap material, are more likely an evidence of the mobility of the material of which the cap is composed.

This is the first description of extra-nuclear caps in the Rhizidiaceae. Their appearance in *E. operculatum* is in general similar to those described by Thaxter (1896), Cotner (1930a), (1930b), Hatch (1935), Matthews (1937) and Karling (1937b) for *Blastocladia*, *Allomyces*, *Blastocladiella* and *Cladochytrium* respectively. The method of origin and the function of the nuclear cap are still matters of dispute. Debasieux (1920) found that following cleavage of *Coelomycidium Simuli* chromatic granules appeared in the segments, fused into a large body, and came to lie at the apex of the nucleus opposite the point of attachment of the cilium. He regarded this as an accessory nucleus, the significance of which is obscure, possibly mitochondrial in origin, having some function in the formation of the cilium. Hatch (1935) describes the nuclear cap as originating by the aggregation, vesiculation and fusion of chondriosomes around the nucleus during sporo- and gametogenesis, and believes it is equivalent to the so-called limosphere in the mosses. Karling (1937b), however, found no evidence of fusing chondriosomes in *C. replicatum* and believes that the cap may have arisen by the aggregation and confluence of chromatic granules or bodies in the cytoplasm. Thus far, I have observed no fused chondriosomes in any stage in the development of the thallus or during sporogenesis of *E. operculatum* by intra-vitam staining with Janus green. Furthermore, that the nuclear cap may be

conspicuously present in material killed in non-chondriosomal fixatives containing acetic acid and other lipoid solvents, militates against the view that it is wholly chondriosomal in origin. Thaxter and Cotner describe what is now known in *Blastocladia* as the extra-nuclear cap as lying within the nucleus, and regards it as a nutritive element, while in *C. replicatum* Karling suggests that it may be utilized as a reserve food in the germination of the zoospore. In *E. operculatum*, as will be shown more in detail later, a mass of material similar in staining reaction to that which composes the nuclear cap may be found in the germ tube and the incipient sporangia at some distance from the nucleus, which suggests that it may have been only partially utilized, and the remainder migrated into the germ tube with the nucleus during germination.

In addition to the nucleus and nuclear cap, in fixed and stained zoospores a fine cytoplasmic strand may often be seen connecting the point of attachment of the cilium with the nucleus, as in figure 6. The nuclear cap in this figure almost surrounds the nucleus, partly obscuring the exact point of contact of this strand. This cytoplasmic strand never appears as sharply defined as those figured in *Allomyces, Blastocladiella, Leptolegnia caudata*, by Hatch (1935), Matthews (1937), Cotner (1930a), and Mathews (1932). Although I have never found it to be double as in the latter genera, it is apparently of the same nature and function as the rhizoplast. At the point of insertion of the cilium on the spore is a minute dark staining region or granule, which is very similar to, but not as sharply defined, as the basal granule or blepharoplast described by Mathews (1932), Curtis (1921), Kusano (1930), and others.

The formation of the cilium was studied only in living material from observations of zoospores released prematurely from sporangia by mechanical means. Ordinarily, the cilium is visible only after the zoospores have been discharged from the zoosporangium and have begun to pull apart from the globular mass of spores. The cilium may, however, have formed earlier, for immature swarmspores forced out of the immature sporangium by mechanical pressure possess structures suggestive of developing cilia. Figures 11 and 12 show what I believe to be developmental stages which were arrested by injury. At the end of the cilium a small vesicle or loop is observed which may be the material which gradually spins out to form the cilium. Similar vesicles have been observed in *Chytridium zygnematis* by Rosen (1887) and Fischer (1892) which they believed to be loops formed by the tips of the cilia, by Kusano (1912) in *Olipidium* and regarded by him as nodules, and by Curtis (1921) and von Minden (1923) in *Synchytrium endobioticum* and *Macrochytrium*

botrydioides. All of the descriptions, however, relate to the disintegration of the cilia rather than to their development.

Biciliate zoospores are rare in *E. operculatum* and seem to be the result of unequal or incomplete cleavage rather than fusion of two uniciliate ones. In figure 13 is shown a large biciliate spore with two highly refringent globules which eventually fuse into a single large globule, as is illustrated in figure 14. Multiciliate zoospores of this type are fairly common in the Chytridiales and have been reported by Lagerheim (1888), Kusano (1912), Ojerholm (1934), Karling (1936b) and others.

Germination of the Zoospore

Germination stages of the zoospore have been studied from living material within *Cladophora* filaments, and in fixed and stained preparations made by sowing zoospores on slides smeared with a film of potato dextrose agar. The zoospores come to rest and the cilia disappear immediately before germination. In one case observed, the cilium disappeared during an amoeboid stage; whether this is the usual behavior of the zoospores cannot be stated definitely, since the process is exceedingly rapid. It is questionable whether the cilium is retracted or whether it is dropped, as Kusano (1930) has described for *Synchytrium fulgens*, and Curtis (1921) claims for *Synchytrium endobioticum*. The zoospore rounds up at once after the cilium is lost, as illustrated in figure 15, and within a few minutes produces a small papilla on the side, as shown in figure 16, which increases in length as shown in figures 17 and 18. The protoplasm changes from the hyaline, semi-transparent appearance of the active

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Explanation of Plate 1

Figs. 1–3. Zoospores, from living material, showing the various positions assumed by the highly refractive globule. Figures 1 and 2 show a structure in the center which may be the nucleus and nuclear cap (×2719).

Fig. 4. Unusually large zoospore from germinated resting spore in amoeboid phase, illustrating the plastic consistency of the highly refractive globule (×2719).

Fig. 5. Zoospore showing vacuole at anterior end, large extranuclear cap and nucleus. From material fixed in Flemming's weak and stained haematoxylin (×3495).

Fig. 6. Zoospore with vacuole in nuclear cap, large nucleus with nucleolus and cytoplasmic connection between nucleus and cilium. From material prepared as in figure 5 (×3495).

Figs. 7–10. Zoospores from material fixed in osmic fumes and stained with iron haematoxylin showing the nucleus and various amounts of extranuclear material surrounding the nucleus (×3495).

Figs. 11, 12. Immature swarmspores showing possible cilium development (×2719).

Fig. 13. Biciliate zoospores with two highly refractive globules (×2719).

Fig. 14. Same as figure 13, a little later, after fusion of highly refractive globules (×2719).
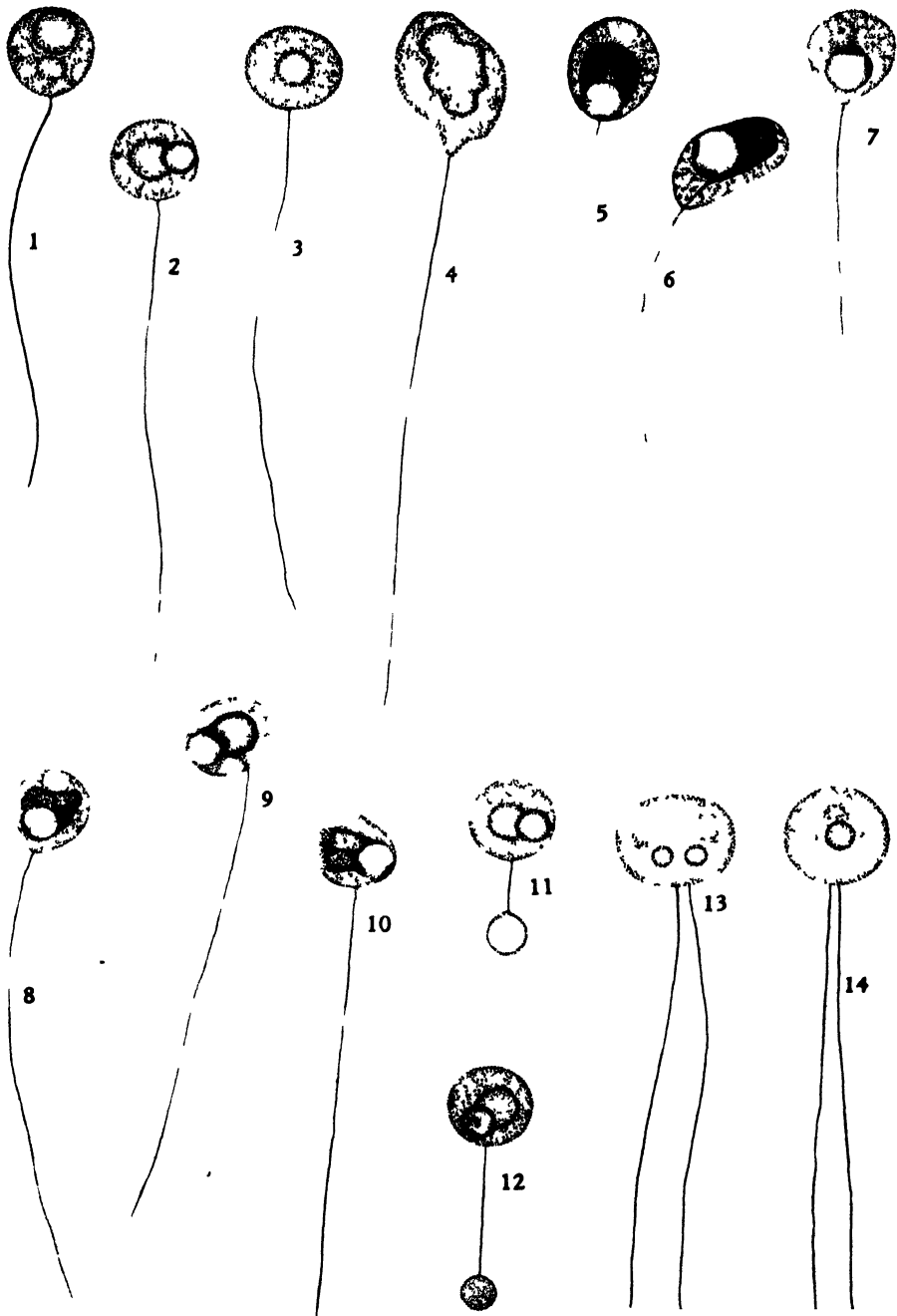
zoospore to a slightly greyish color with the still-distinct refractive globule.

The nucleus and nuclear cap likewise undergo some optical change and are not so sharply defined as in the active zoospore. In the initial stages of germination, observed in fixed and stained preparations, the nucleus and nuclear cap remain in the zoospore as illustrated in figures 19 and 20. The germ tube develops as a fine filament, as in figure 21, and often attains a length of 43μ before branching or forming the rudiment of the zoosporangium. The tip of the germ tube usually forms the main axis of the rhizoidal system and branching may occur, as in figure 22, before the appearance of the incipient sporangium.

The spores often form more than one germ tube on agar as Karling (1937a) has already shown, but the sporangium develops in only one of them. Which of these germ tubes shall give rise to the sporangium seems to be determined by the final position of the spore nucleus. If the zoospore is binucleate, however, and forms two or more germ tubes, two sporangia may be formed, provided that the nuclei migrate into different tubes, but I have never seen this occur. Occasionally the young thalli have the appearance shown in figures 32 and 46, which suggests that branching may have occurred at the side of the rudimentary sporangia. But, as Karling (1931) has pointed out in the case of *Entophlyctis*, this appearance may have come about by the development of the incipient sporangium at the juncture of two or more branches of the germ tube. As the rudiment of the sporangium begins to enlarge, the branches are carried farther apart so as to give the appearance noted above. Branches may actually grow out from the rudiments in the early stages of develop-ment, as is shown in figures 32 and 46. Branching of the germ tube and the genesis of the rhizoidal system may take place before the formation of the swelling which is to become the sporangium, as in figure 22, or after, as in figures 24 and 25. As far as my present observations go, it seems to occur before, as has been shown for *Diplophlyctis*, *Entophlyctis* and *Nephrochytrium* (Karling 1930, 1931, 1938a).

The nucleus and nuclear cap do not begin to migrate to the swelling immediately upon germination, but usually remain in the zoospore until the germ tube is well developed, as illustrated in figure 27. It has not been possible to establish a definite relationship between the time of the arrival of the nucleus and the local enlargement of the germ tube. In figure 26 the nucleus is shown in a long germ tube and in figure 28 two nuclei are shown in the branched germ tube, but as yet no swelling has occurred.

Figures 29 to 32 show conspicuous swellings, but it is impossible to tell whether these were formed before or after the arrival of the nuclei. In figure 33, although a definite swelling is already apparent in the germ tube, the nucleus and nuclear cap are still within the zoospore. This would indicate that the initial stages of swelling are not dependent upon the presence of the nucleus in that region. In figure 28 the lower nucleus in the germ tube may have a nuclear cap or some extra-nuclear material on one side, and between the second nucleus and the old zoospore is also a large amount of heavily staining material. Whether or not this is extra-nuclear cap material which has been carried down with the nuclei is not certain, but it is quite chromatic and stains intensely like the nucleole. Binucleate thalli like those in figures 28 and 32 occur rarely

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Explanation of Plate 2

Fig. 15. An unusually large zoospore from resting spore sporangium rounded up ready for germination ($\times 1040$).

Figs. 16–18. Stages in the development of the germ tube ($\times 1040$).

Fig. 19. Early stage in germination, from fixed and stained material showing nucleus and nuclear cap ($\times 1040$).

Fig. 20. Early stage similar to figure 19 but greatly magnified ($\times 2330$).

Fig. 21. Stages in germination, from living material showing the long filamentous germ tube ($\times 1040$).

Fig. 22. Branching of germ tube to form the initial rhizoidal system ($\times 1040$).

Fig. 23. Same as figure 22 a little later showing the initial swelling in the germ tube ($\times 1040$).

Fig. 24. A slightly later stage in which the contents of the zoospore have migrated into the sporangium ($\times 1040$).

Fig. 25. Initial swelling in unbranched germ tube ($\times 1040$).

Fig. 26. Early germination stage, from fixed and stained material showing the migration of the nucleus. ($\times 1040$).

Fig. 27. Long germ tube with nucleus remaining in the zoospore ($\times 1040$).

Fig. 28. Germination stage showing two nuclei migrating into the germ tube ($\times 1040$).

Fig. 29. Early germination stage, from fixed and stained material showing nucleus in incipient sporangium ($\times 1040$).

Fig. 30. Type of branching of germ tube which is frequently found when zoospores germinate on agar ($\times 1040$).

Fig. 31. Normal type of rudimentary thallus, with the nucleus in the swelling and a large amount of extranuclear chromatic material in the old zoospore case. ($\times 1040$).

Fig. 32. Binucleate incipient sporangium ($\times 1040$).

Fig. 33. Germination stage from living material showing gradual vacuolization of the zoospore ($\times 1040$).

Fig. 34. An early germination stage, from fixed and stained material showing the enucleate, primary swelling ($\times 1040$).

Fig. 35. An early germination stage showing the nucleus in the primary swelling. The relative sizes of the nucleus and germ tube indicate that nucleus probably elongates during its migration through the germ tube. ($\times 1040$).

Fig. 36. Sporangium developing adjacent to the zoospore without the formation of a long germ tube ($\times 1040$).

Fig. 37. Germination stage, from material grown in *Nitella*, and fixed and stained showing nucleus and extranuclear chromatic material in the swelling ($\times 2330$).
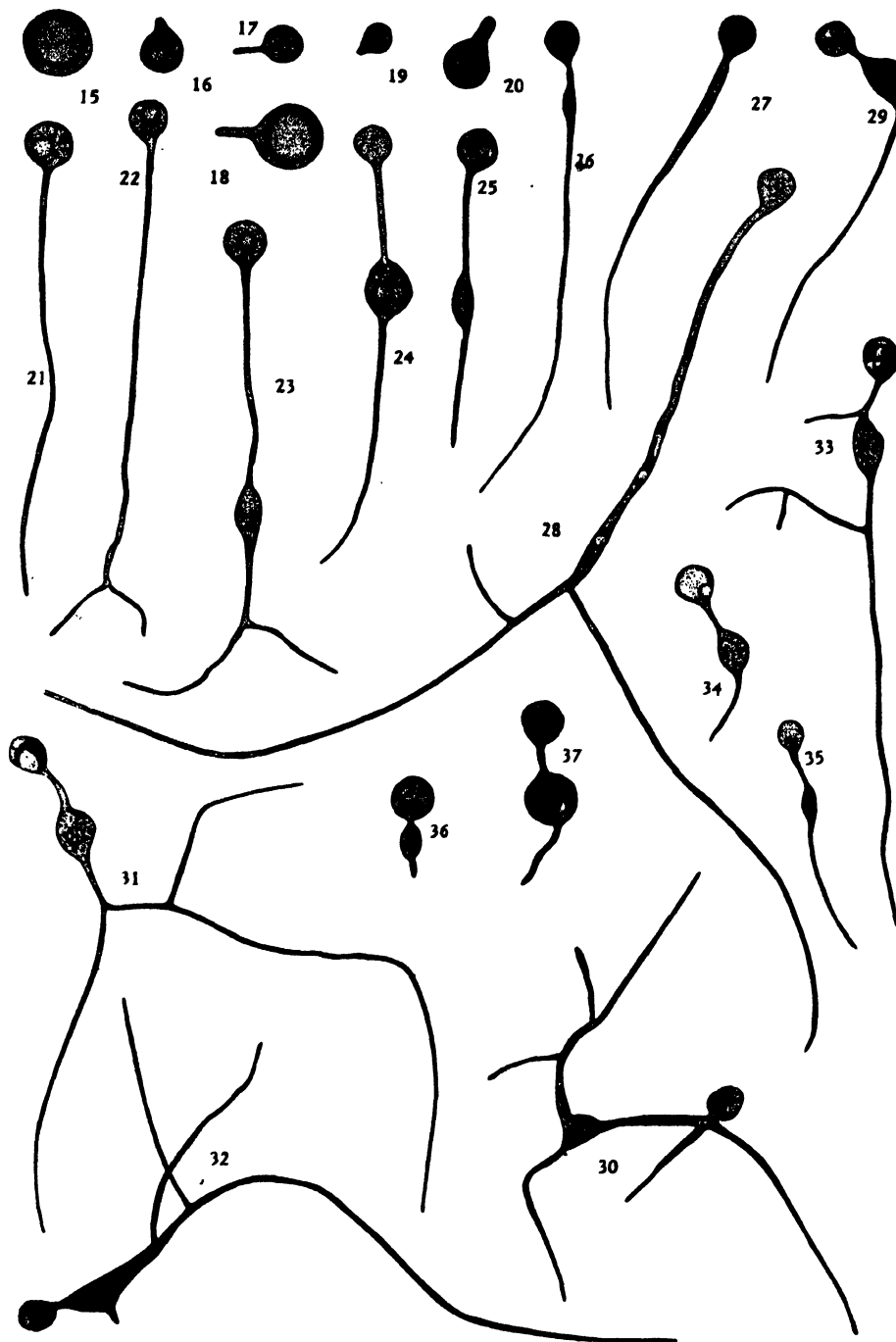
and may have arisen from a large binucleate spore or by division of the zoospore nucleus, although so far I have not found the zoospore nucleus dividing in the spore itself or during transit in the germ tube. The more normal type of development is that shown in figures 29 and 31. The large amount of heavily stained material in the zoospore of these figures and figure 30 suggests that perhaps the nuclear cap had been left behind, since none is visible around the nuclei in the incipient sporangia. It may, nevertheless, relate to the refractive substance of the zoospore which has not been completely dissolved in the process of fixing and staining.

Vacuolation of the cytoplasm occurs as the nucleus moves down into the germ tube, until the zoospore case becomes empty, as in figures 24, 28 and 29. In living material the refringent material usually remains in the zoospore until most of the other contents have moved down the germ tube, as in figure 34. Small amounts of the substance are observed in the germ tube, and the globule may become broken up into smaller globules, as Karling (1930) has shown in *Diplophlyctis*. As has been already noted with reference to figure 28, there is a considerable amount of densely stained material in the germ tube, and strands of it between the two nuclei, all of which is probably the residue of the refringent material.

The appearance of the nucleus in figure 26 and of the two nuclei in figure 28 suggests that the nuclei pass down the germ tube to the swelling without any apparent change in size or shape. In these figures the germ tube is quite large and readily accommodates the spherical nuclei, but in instances like those shown in figures 31, 35 and 37 the nucleus doubtless became elongated and very slender in transit, as has been shown for *C. replicatum*.

The germination and early development of the thallus described above appears to be the normal and usual type. In a manner unlike that of *Rhizophidium*, *Tylochytrium* and *Phlyctochytrium*, the center of growth, development and organization of *Endochytrium* is transferred by the migration of the nucleus from the zoospore itself to an intercalary swelling which eventually becomes a sporangium or a resting spore. This type of germination and the provision of an intramatrical center is perhaps an adaptation to place the thallus in a more favorable position relative to its food supply. When zoospores are liberated and germinate within the host cell, the distance between the zoospore case and the swelling in the germ tube may be short, as shown in figure 36, and in some cases lacking altogether, whereby the zoospore itself may enlarge and grow directly into a sporangium or a resting spore. I have not actually observed the

developmental stages of such thalli, but the presence of a number of resting spores closely packed together in an old sporangium in figure 100 suggests that they have been formed directly from the zoospores. In such exceptional cases we would thus have the same type of development as in *Rhizophidium*, *Tylochytrium* and *Phlyctochytrium* where the enlarged zoospore becomes the center of growth, development and organization. Certain genera of chytrids doubtless have a predominant type of development which, however, may vary under special conditions and approach that of another type. In *Rhizophlyctis*, for example, the sporangium is reported to have grown directly from the zoospore occasionally, and in *R. Liguicola* (Lindau) Minden it may form as an outgrowth of the zoospore.

Development of the Sporangium

After germination of the zoospore and the establishment of the young thallus, the swelling begins to enlarge into the incipient zoosporangium. This enlargement seems to keep pace with the growth, branching and extension of the rhizoidal system. I have not studied their relative growth rates, but evidently the growth of the sporangium is more rapid after the rhizoidal system has become well established. Following its arrival in the incipient sporangium, the nucleus usually enlarges to a diameter of 3.5μ to 5μ before division, without showing any marked changes in structure. The nucleus before enlargement is spherical and almost empty except for a crescentic nucleolus surrounded occasionally by a well defined nuclear cap as is shown in figure 46. Figure 47 shows an intermediate stage in nuclear enlargement, and figure 48 a later stage in which the primary nucleus has almost doubled its size. With the increase in size of the sporangium and nucleus, the cytoplasm appears to be more vacuolate probably

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Explanation of Plate 3

Fig. 38. Initial stage in the development of the sporangium as observed in living material ($\times 1560$).

Fig. 39. Enlargement of the developing sporangium with large vacuole and highly refractive globules ($\times 1560$).

Fig. 40. A later stage showing an increase in the number of globules ($\times 1560$).

Fig. 41. Second stage in the development of the sporangium showing the gradual dispersion of the highly refractive globules ($\times 1560$).

Fig. 42. Third stage of sporangial development showing the refractive material in the highly dispersed, granular stage ($\times 1560$).

Fig. 43. Beginning of third or maturation stage of sporangial development. Faint lines suggesting cleavage have appeared in the finely granular protoplasm ($\times 1560$).

Fig. 44. Later stage showing formation of highly refractive globules of the zoospore initials ($\times 1560$).

Fig. 45. Mature sporangium containing zoospores ready to be discharged ($\times 1560$).
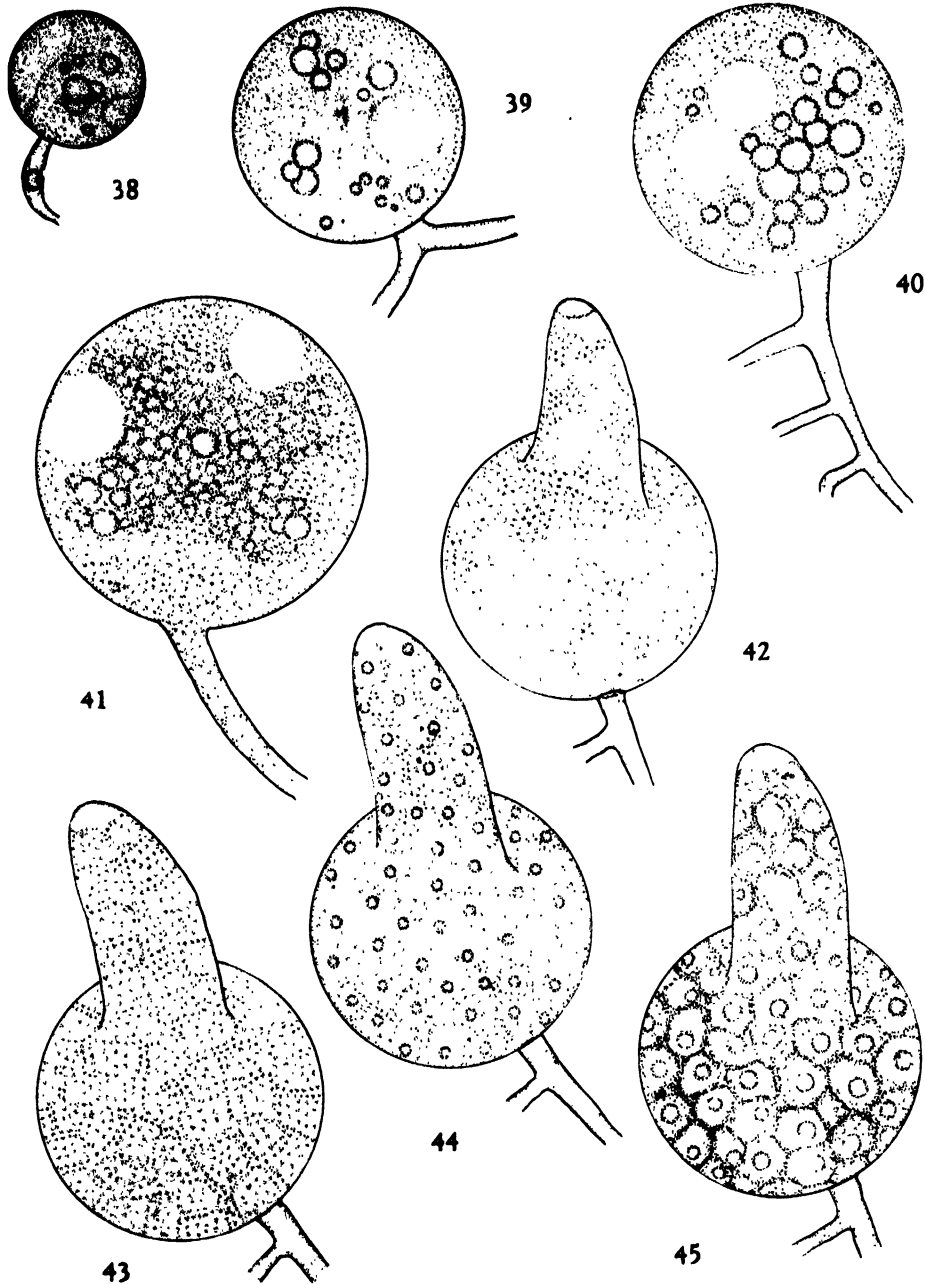
because of the dissolution of the highly refractive globules during fixation. While enlargement of the sporangium proceeds, as observed in living material, there is an increase in the amount of highly refractive material as shown in figures 38, 39, 40. On the basis of size, figure 38 corresponds to figure 50 or 51 of the fixed and stained thalli, while figures 39 and 40 may be comparable to figure 52. Except for comparative size, I have not found any criterion by which to connect stages in the living material with similar stages in the fixed and stained preparations. I shall, therefore, give a brief description of sporangial development in living material and supplement it with my observations on fixed and stained preparations.

The development of the evanescent sporangium may, for convenience of description, be divided into three stages according to the character of the protoplasm, particularly of the highly refractive substance. The first stage may be considered to be the local swelling of the germ tube and the arrival of the nucleus, as shown in figures 29 and 31, a stage characterized by an increase in the amount of highly refractive substance coincidental with the enlargement of the sporangium as shown in figures 38 to 40. The highly refractive material in the form of globules tends to collect in the hyaline protoplasm near the center of the sporangium. One or more large vacuoles may be present, as shown in figure 40.

The second stage in the development of the sporangium relates to the gradual dispersion of the highly refractive globules. As the sporangium enlarges, the globules in their central arrangement become irregular in shape, as shown in figure 41, and break up imparting to the hyaline protoplasm of the maturing sporangium an even and finely granular appearance, as shown in figure 42. The protoplasm at this time is greyish-white as Karling (1938d) has observed in a similar stage of *Rhizophidium laterale*. The optical appearance of the process of dispersion seems to be similar to that described by Couch (1935) in *Phlyctidium anatropum*. He describes it as a digestion of the large globules and questions his own description of these bodies as being composed of fat.

The third stage, illustrated in figures 43–45, relates to maturation and zoosporogenesis. The minute granules formed in the second stage appear to coalesce, forming slightly larger granules. These arrange themselves, as in figure 43, chiefly along the borders of segments which may represent the zoospore initials.

A similar condition has been shown in *Rhizidiomyces apophysatus* and *Diplophlyctis intestina* by Zopf (1884) and in *Nephrochytrium* and *Endochytrium digitatum* as observed by Karling (1938a, 1938b). Figure

44 shows zoospore globules. Ultimately, as shown in figure 45, all the refractive substance becomes localized in the characteristic globules of the zoospore. This process of coalescence has been described in the development of the zoospores of *Polyphagus Euglenae* (Wager 1913), *Rhizophidium globosum* (Couch 1932) and *R. Lagenaria* (Sparrow 1936). The zoospores in figure 45 are about to be discharged from the zoosporangium and, probably because of their imbibition of water, they are pressed together firmly in somewhat polygonal shapes.

At the tip of the exit tube is a clear region that emits a hyaline viscid fluid at the time of the discharge of the zoospores. In the sporangium from which figures 42–45 were drawn, the operculum did not become noticeably thickened, but it was clearly evident following the discharge of the zoospores.

The early developmental stages as seen in fixed and stained material are shown in figures 46 to 52. These seem to correspond to the first stage described in the living material. In figure 46 the nucleus has arrived in the swelling, and in figures 46–47 it is increasing in size until in figure 48 it has become three times the size of the zoospore nucleus. The cytoplasm in some cases, as in figure 47 and the binucleate sporangia of 49 and 50, may be vacuolated. The four and sixteen nucleate stage is shown in figures 51 and 52. Since the cytoplasm in this stage does not contain the large vacuoles present in figures 39–41 of the living material, it is assumed that this is a later stage than that drawn in figures 39–41.

It is noticeable that no nuclei have been present in the rhizoids. Figure 50 is merely an apparent exception. In the basal part of this rhizoid there is a heavily stained body which might resemble a third nucleus, but since division is simultaneous within the sporangium, it would be expected that either two or four nuclei would be present instead of three. The only explanation would be that division in one of the original two nuclei had been delayed. It is my belief that this body is chromatic

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Explanation of Plate 4

Fig. 46. Early stage in the development of the thallus, soon after the arrival of the nucleus in the incipient sporangium, from fixed and stained material ($\times 920$).

Figs. 47, 48. Later uninucleate stages in the development of the thallus with the nucleus increasing in size ($\times 920$).

Fig. 49. Binucleate stage of the developing thallus ($\times 920$).

Fig. 50. Binucleate stage in the development of the thallus showing possible extranuclear material in the base of the rhizoid ($\times 940$).

Fig. 51. Four-nucleate stage with enucleate rhizoid ($\times 920$).

Fig. 52. Sixteen-nucleate stage. The rhizoid is continuous with the sporangium and no nuclei have yet appeared in the rhizoid ($\times 920$).
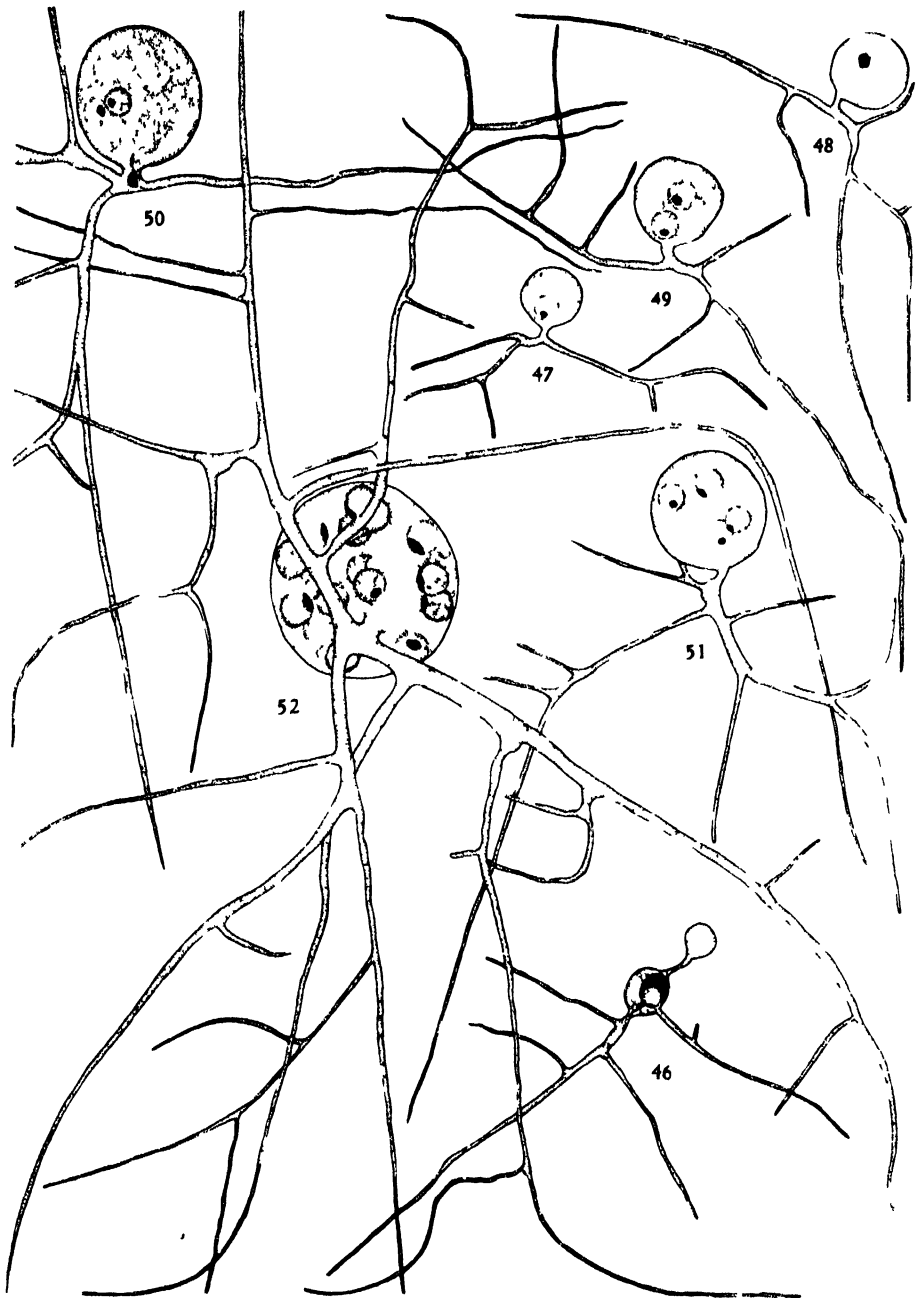
material which has remained in the rhizoid, since the examination of over one hundred additional whole mounts of thalli in various stages of development has failed to reveal the presence of nuclei in the rhizoids.

The rhizoid is continuous with the sporangium during the developmental stages, and its protoplasm contains highly refractive globules, but as the sporangium reaches the granular stage, the rhizoid is separated from the sporangium by a septum and is optically homogeneous. Furthermore, in fixed and stained preparations as shown in figure 71, there is some cytological evidence of protoplasmic flowing especially at the basal part of the rhizoid where deeply staining bodies have been drawn out to form strands. In view of these observations it seems logical to conclude that the protoplasm has flowed from the rhizoid into the sporangium prior to the formation of the septum.

Nuclear Division

Nuclear division in the evanescent sporangia is simultaneous, as illustrated in figure 68, and mitotic. The division spindles in figure 68 are oriented in several planes so that both profile and polar views of equatorial plate stages are visible. The spindle is intranuclear, and at its poles characteristic cone-shaped bodies are present. Since distinct astral rays are frequently oriented on these bodies, the latter doubtless function as centrosomes. The vacuolated cytoplasm and the relatively great distance between the nuclei would indicate that this sporangium was in an intermediate stage in development which is characterized in living material by the presence of many highly refractive globules.

In figure 53 is shown a nucleus which I believe to be in a resting stage or in a very early prophase. Within the nucleus is a large, lens-shaped nucleolus lying against the nuclear membrane. The chromatin reticulum, consisting of irregular strands, is faintly stained and appears in a more continuous background. The nucleus shown in figure 54 with a flat, ring-shaped nucleolus is possibly an early prophase stage. The chromatin bodies are larger, more sharply defined, and are connected by faint strands which may be linin threads.

Spireme stages in which the nucleole lies flattened against the side of the nuclear membrane are shown in figures 55 and 56. A later stage is shown in figure 57. The thick, irregular and elongate strands are clearly defined and look like the early stages of chromosome formation. These become more distinct and stand out as short, elongate rods before there is any indication of the achromatic spindle, as is shown in figures

58 and 59. The ring-shaped nucleolus is prominent in figures 58 and 59, and in figure 60 in an optical view is shown to be vacuolated. The ring-shaped nucleolus as found in *E. operculatum* is very similar to that described by Karling (1937b) for *Cladochytrium replicatum*. In the metaphase the nucleolus is reduced to a round, flattened body which lies at the nuclear equator and against the membrane, as shown in figure 63. It appears to differ in size and shape in various nuclei, becoming quite indistinct in figure 65 and in the anaphase shown in figure 66, but quite prominent in the late anaphase shown in figure 67.

As has been noted above, densely staining, cone-shaped bodies may be found at the poles of the nucleus and the division figure as in figure 56a. These structures may be initial stages in the formation of the central bodies which are prominent at the poles of the spindles in figures 61 and 62 and particularly in figures 63–65. The central bodies are not as sharply defined as those shown by Harper (1897) and (1905) in *Erysiphe* and *Phyllactinia* and do not have such bushy and dense astral radiations. In figure 61 the astral rays are short, while in figure 62 they are long. The central bodies shown in figure 64 resemble those of *Polyphagus Euglenae* (Wager 1913). Centrosome-like bodies have been reported by Hovasse (1936) at the poles of the intra-nuclear spindle of

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Explanation of Plate 5·

Fig. 53. Resting nucleus with lens-shaped nucleole and faintly staining chromatin reticulum (×4167).

Fig. 54. Prophase stage with chromatin reticulum showing the ring-shaped nucleolus (×4167).

Figs. 55, 56. Spireme stages.

Fig. 57. Late prophase stage (×4167).

Figs. 58, 59. Late prophase stages showing chromosomes (×4167).

Fig. 60. Face view of the ring-shaped nucleolus in prophase stage (×4167).

Fig. 61. Prophase stage with central bodies and short astral rays (×4167).

Fig. 62. Prophase stage with central bodies and extensive astral rays (×4167).

Figs. 63, 64. Metaphase stages showing central bodies at the poles of the intranuclear spindle (×4167).

Fig. 65. Metaphase stage showing poles of intranuclear spindle extended through the nuclear membrane (×4167).

Fig. 66. Anaphase stage (×4167).

Fig. 67. Late anaphase, region of old nucleus still discernible (×4167).

Fig. 68. Section of evanescent zoosporangium showing simultaneous nuclear division (×1300).

Fig. 69. Progressive cleavage of protoplasm of evanescent zoosporangium (×1300).

Fig. 70. A portion of a section through a zoosporangium showing polygonal zoospore initials (×1300).

Fig. 71. Section through developing evanescent sporangium showing lines of flow of protoplasm from the rhizoids (×1300).
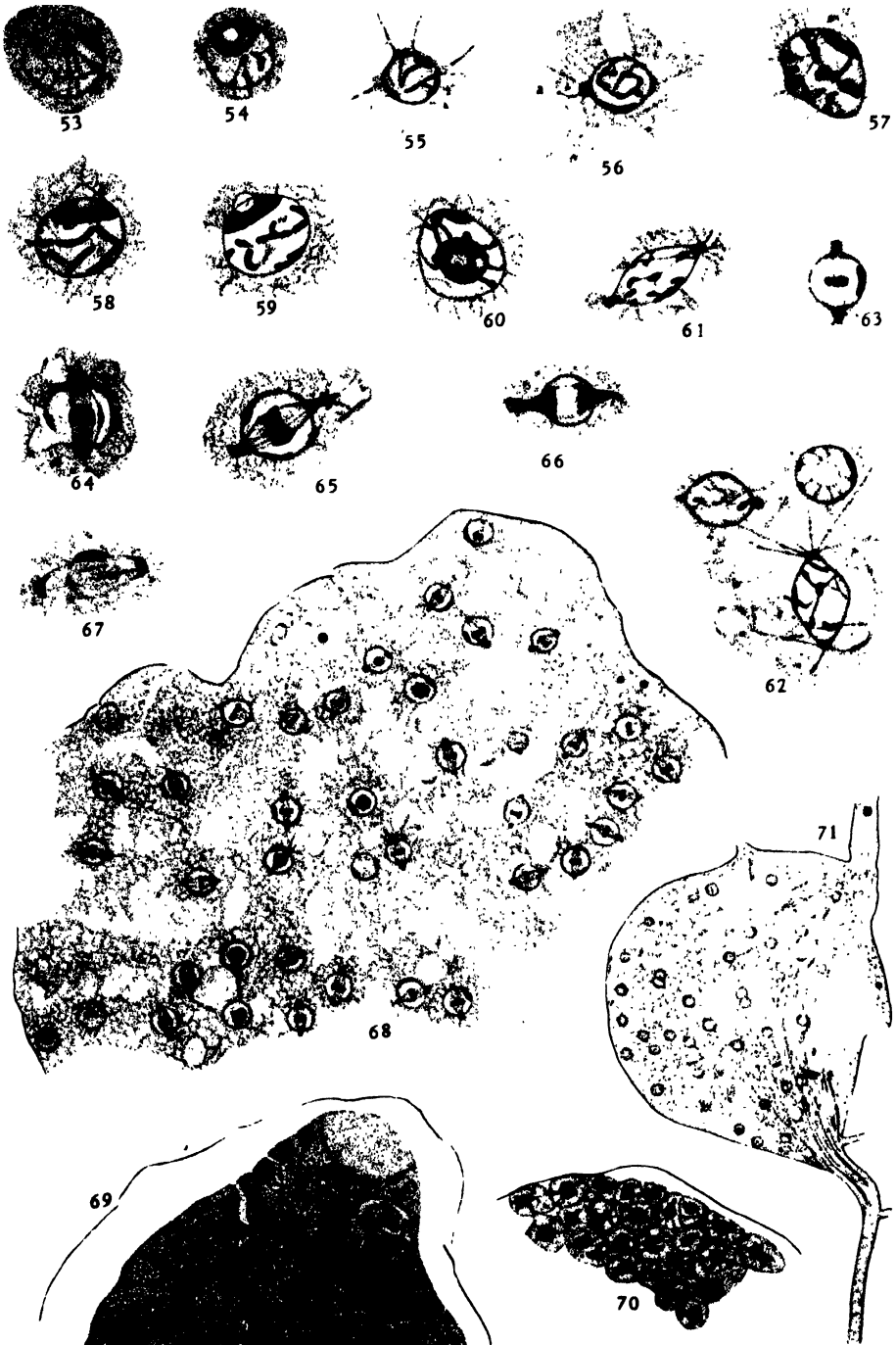
Rhizophidium Beauchampi but these are rather indistinct and do not appear to resemble those of *E. operculatum.*

The spindle of *E. operculatum* is intra-nuclear, a characteristic common to most of the chytrids except *Olipidium Brassicae* (Nemec 1912), *O. radicale* (Schwartz and Cook 1928), *Cystochytrium radicale* (Cook 1932) and the resting spores of *Olipidium Vicae* (Kusano 1912), species which belong in the Myxochytridineae. The chromosomes in the equatorial plate stage shown in figures 63 and 65 are so close together that the individual chromosomes are not distinguishable. The poles of the spindle appear to extend through the nuclear membrane but this appearance may be caused by the large central bodies at these points. This spindle structure is similar to that described for *Polyphagus Euglenae* (Wager 1913) in which the astral rays extend through the nuclear membrane. The spindle shown in figure 64 has a reduced central body similar to that shown by Karling (1937b) in *Cladochytrium replicatum.* In the anaphases, the poles of the spindle extend through the nuclear membrane as in figure 66. The blunt, irregular apex of the spindle suggests that restricted astral rays may be present.

A late anaphase stage is shown in figure 67 with a heavily stained chromosome group now lying at the poles of the spindle. The nuclear cavity is faintly outlined in the cytoplasm, possibly by the remnants of the nuclear membrane.

Zoosporogenesis in the primary evanescent sporangium

The cleavage of the sporangium of *E. operculatum* to form the uniciliate zoospores is by progressive furrowing. Since the process of delimitation of the zoospores in this species is essentially similar to that described for many algae and fungi with sporangia, it will be dealt with briefly. Cleavage of the protoplast apparently begins soon after the large highly refractive granules have become dispersed throughout the entire cell as minute granules in the way described earlier. The hyaline protoplasm makes identification of the cleavage furrows uncertain and the evidence based entirely upon the reorganization of the granules does not seem to me to be sufficient to identify the granular stage with the beginning of cytokinesis.

Cleavage furrows, as they appear in fixed and stained material are shown in figure 69. The furrows proceed centripetally from the margin of the protoplast and in various directions from clefts which originate within the center of the protoplast as described by Harper (1899) in the

formation of the protospores of *Pilobolus Crystallinis, Synchytriu n decipiens* and the spores of *Sporodinia grandis.* They are likewise similar to those of *Rhizopus nigricans* and *Phycomyces nitens* Swingle (1903). Progressive cleavage as found in *E. operculatum* agrees with most ob-servations on the Phycomycetes and since these have been summarized frequently by Harper (1899), Swingle (1903), Schwartz (1922), Bold (1933) and Karling (1937b) they need not be discussed here.

The zoospore initials soon after their formation may assume a polygo-nal shape as shown in figure 70 which may be comparable to the mature stage of the living material shown in figure 45. This shape is due to pressure resulting from the intake of water following cleavage such as Harper (1899) has found to occur in *Synchytrium decipiens* and *Sporo-dinia grandis.* Schwartz (1922) has observed the zoospores of *Olpidiopsis Saprolegniae* to become swollen following their delimitation, a phenom-

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Explanation of Plate 6

Figs. 72–80. Stages in the development of a smooth-walled resting spore, from living material, showing at intervals the fusion of the highly refractive globules ($\times 975$).

Fig. 81. Mature smooth-walled resting spore showing large central refringent globule ($\times 975$).

Fig. 82. Mature resting spore showing the empty zoospore case with germ tube and unbranched rhizoid ($\times 975$).

Fig. 83. Early stage in resting spore formation, from material fixed and stained *in toto* ($\times 975$).

Figs. 84–86. Developmental stages of resting spore, from fixed and stained material, showing increased vacuolation of protoplasm ($\times 975$).

Fig. 87. Median optical section of mature resting spore, showing nucleus in peripheral layer of protoplasm ($\times 975$).

Fig. 88. Resting spore in advanced stage of development showing a binucleate con-dition ($\times 975$).

Fig. 89. Small mature resting spore showing chromatic granules in the cytoplasm ($\times 957$).

Fig. 90. Surface view of protoplasmic layer of mature resting spore, from fixed and stained material ($\times 975$).

Fig. 91. Median optical section of living mature resting spore which has developed within an evanescent sporangium and showing protoplasmic layer surrounding the central globule ($\times 975$).

Fig. 92. Surface view of protoplasmic layer of living resting spore ($\times 975$).

Fig. 93. Germinated resting spore showing the three layers of the wall and empty sporangium ($\times 975$).

Figs. 94–96. Stages in the formation of a rough wall of a resting spore showing the dead host protoplasm and the shrinkage of the initial wall from it ($\times 975$).

Fig. 97. Surface view of rough-walled resting spore ($\times 975$).

Fig. 98. Median optical section of thick-walled resting spore, from living material ($\times 975$).

Fig. 99. Median optical section of resting spore showing heavily lobed wall ($\times 975$).

Fig. 100. Resting spores and degenerated zoospores within an evanescent sporangium ($\times 975$). `
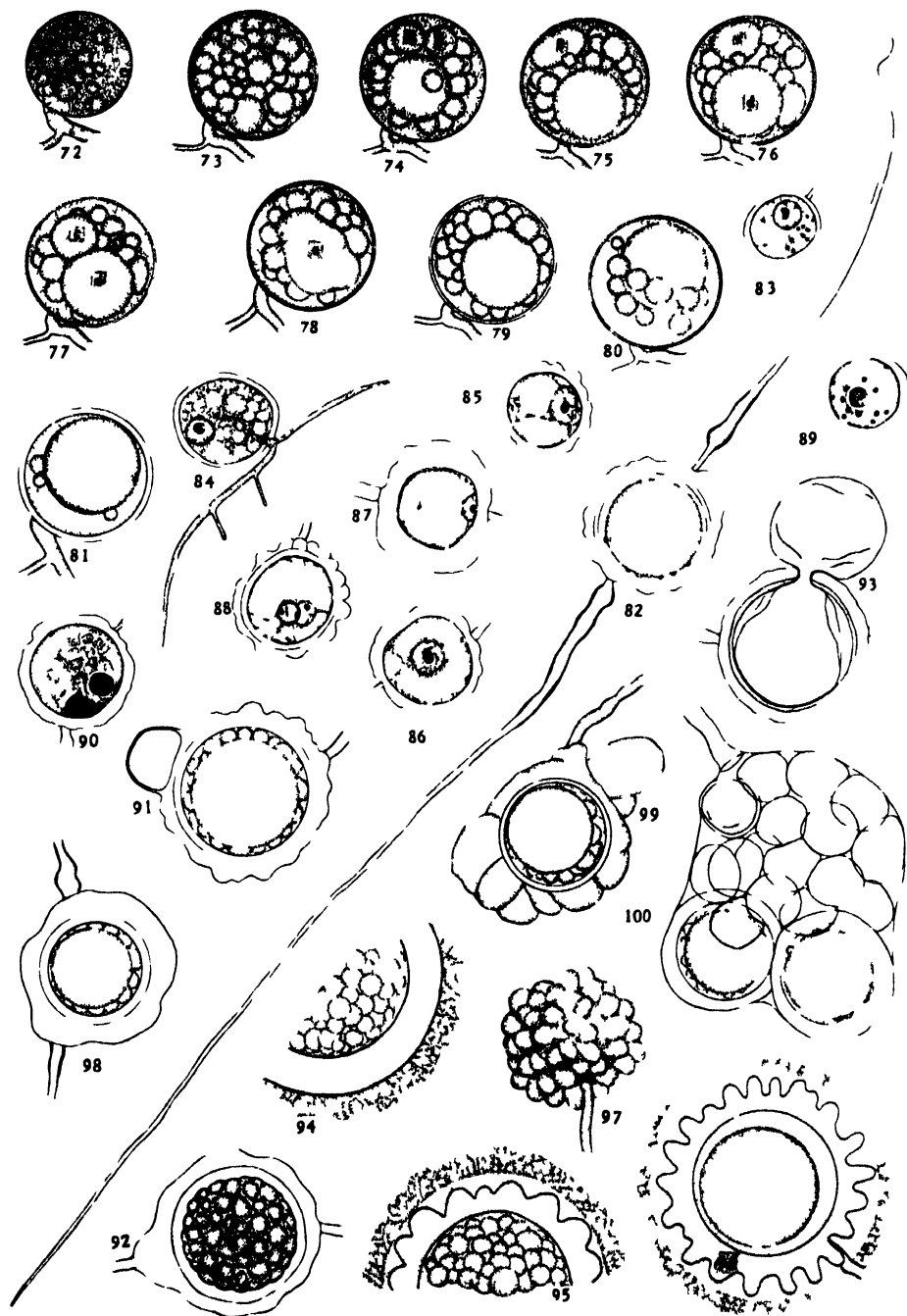
enon which appears to occur frequently in the maturation of Oomycetes
and Zygomycetes.

The nuclear cap material is present in the zoospores of the polygonal
stage shown in figure 70 but it was apparently not present in the initial
cleavage stage of figure 69. This would indicate that nuclear cap forma-
tion in *E. operculatum* takes place following the initiation of cleavage
furrows and at about the same stage in development as the deeply stain-
able material as observed in the zoospores of *Polyphagus Euglenae*
(Wager 1913). Similarly the nuclear cap of *Allomyces arbuscula*
(Hatch 1935) and *Cladochytrium replicatum* (Karling 1937b) appears
to become discernible following the initial cleavage stage.

The structure and germination of the resting spore

The development of the resting spore.—The resting spores of
E. operculatum were described by Karling (1937a) as being smooth or
rough-walled, and my study confirms these observations. As is shown in
figures 81, 91 and 97, the wall may be smooth and relatively thin or thick,
rough and warted. The thickening of the wall may take the configuration
of lobes, as in figure 99, or it may be very irregular and uneven as in
figure 98. It may even envelop a considerable part of the germ tube as in
figure 92.

Resting spores form abundantly in old cultures to which no new fila-
ments of *Cladophora* or fresh water have been added for about three
weeks. Under these conditions the developing evanescent sporangia de-
crease in size and number and resting spores appear in increasingly large
numbers. These resting spores develop either *in situ* within evanescent
sporangia which fail to discharge their spores, or directly from germinat-
ing zoospores.

The young thalli which give rise to resting spores are similar to those
which give rise to evanescent sporangia and cannot be distinguished until
the local enlargement of the germ tube has reached considerable size. The
first indication of resting spore development is a gradual increase in the
number of highly refractive globules without a corresponding increase in
the cell size. Figures 72 and 73 illustrate a developing resting spore ob-
served at an interval of 19 hours. Although the structure in figure 72
might conceivably be either an evanescent sporangium or a resting spore,
however, in figure 73 it is positively identified as a resting spore by the
abundance of highly refractive globules. The globules coalesce gradually
as is illustrated in figures 74 to 80. Two adjacent globules of equal size,

figures 74 a and b, fuse to form the elongated globule of figure 75c. This globule began to round up in figure 76c and fifteen minutes later it came in contact with the large globule of figure 77d. Fusion took place ten minutes later, momentarily forming the irregular body shown in figure 78e. Within two and one-half hours the majority of the globules had fused with this larger one as shown in figures 79 and 80. In the mature resting spore, figure 81, a few small globules which had failed to coalesce are shown at the side of the large globule. A mature resting spore thallus of limited size is shown in figure 82. The old zoospore and germ tube are still present at one side of the resting spore and opposite to this is a long unbranched rhizoid. Branching of the rhizoid occurs frequently in the resting spore but not to the same extent as in the thalli which bear evanescent sporangia. It is to be noted in figure 82 that the walls of the germ tube and the rhizoid are thickened locally but thin out at the point of attachment with the resting spore. The formation of a large number of refringent globules in the development of the resting spore and their coalescence to form one or more larger ones, as has been described above, is fundamentally similar to that already reported for *Cladochytrium replicatum, Chytridium lagenaria, E. operculatum, E. digitatum, Nephrochytrium appendiculatum, Chytridium aggregatum* and *Rhizophidium macrosporum* (Karling 1935, 1936b, 1937a, 1938a, 1938b, and 1938c).

In fixed and stained material the refringent globules, as such, are no longer visible and the substance of which they are composed is apparently dissolved during preparation. An early stage in the development of a smooth walled resting spore is shown in figure 83 and probably represents the condition preceding the accumulation of highly refractive globules. In figures 84 to 86 are slightly later stages from material fixed in Allen and Wilson's fixative and stained *in toto* with methyl blue and acid fuchsin in lacto-phenol. Figure 84 shows an early stage with a large number of small vacuoles in the cytoplasm which may have been left by the dissolution of the refringent globules. The nucleus of this resting spore is quite large and distinct with a conspicuous nucleole. A later stage is represented in figure 85 in which the vacuoles have increased in size and the nucleus and cytoplasm have been displaced towards the periphery of the cell, possibly by the gradual fusion of the globules. Figure 86 corresponds perhaps to figure 76 of the living material and the strands of cytoplasm shown here may be those which ran between the large globules of the living material. A mature resting spore is shown in figure 87 in which the protoplasm has been displaced to the periphery of the cell and the nucleus is

somewhat flattened against the wall. The latter figure and also figures 88 to 90 were drawn from material fixed in Allen and Wilson's and stained *in toto* in Heidenhain's haematoxylin. Surrounding the nucleus and distributed through the cytoplasm are small heavily staining granules which are also shown in figures 83, 86, 88 and 89. These appear to be similar to the basophilic and chromatic granules found in the resting spores of *P. Euglenae, S. fulgens* and *C. replicatum* (Wager 1913, Kusano 1930, and Karling 1937b). The resting spore shown in figure 90 is, I believe, an old one and in surface view the protoplasm appears to have the same honeycomb appearance which is often clearly evident in old living spores, as in figure 92. Figure 90 shows a view of the protoplasmic layer, which, in living material shown in median optical section in figure 91, appears as a layer of smaller globules surrounding the central mass. This layer was at first believed to consist of highly refractive globules that had not coalesced with the large one, but under microchemical tests it fails to give the same fat or oil reaction as the highly refractive substance, and is not dissolved upon fixation. In fixed and stained preparations, as shown in figures 89 and 90, a fairly large body which stains densely in haematoxylin and Feulgen's is often present in the peripheral cytoplasmic layer of such old spores.

The wall of the resting spore is composed of three layers, as shown in figure 93. The outer layer or epispore is thick and stains brilliantly with orange G., while the thinner middle wall or mesospore, indicated by the stippled region, stains blue in lacto-phenol with acid fuchsin and cotton blue. A thinner membranous endospore that may be observed in resting spores which have germinated is particularly evident in figure 93, where it has been separated from the mesospore. In the early stages in the formation of the rough or warted wall, a broad, hyaline region surrounds the resting spore and has its outer margin against the host protoplasm as shown in figure 94. Whether or not this region is derived by the secretion of a mucilagenous material as Kusano (1930) has described in *Synchytrium fulgens* or by the digestion of the host protoplasm as Miss Curtis (1921) has described in *Synchytrium endobioticum* is uncertain. The subsequent stages in the development of the wall appear to be accomplished by the gradual shrinkage and transformation of the hyaline substance, first into rather broad warts, as shown in figure 95, and later to more sharply lobed processes separated from the host protoplasm as shown in figure 96. The wall substance as it matures becomes more yellowish and opaque. It is possible, however, that the wall is not formed by the infolding of the

hyaline substance but that it develops as an outward growth from the resting spore into the hyaline region. The wall of the resting spore appears to be derived from the fungus rather than from the host protoplasm, as indicated by the fact that neutral red stains the host protoplasm heavily while the wall itself shows no reaction. This test, however, is not conclusive as it is possible that, if the wall is derived from the host, changes in its composition would occur which would also change the staining reaction. The rough-walled spore appears in median optical section as in figures 96, 98 and 99, and in surface view as in figure 97. In fixed and stained preparations the hyaline unlobed stage in wall development, figure 87, may correspond to figure 94 of the living material. At this stage the wall seems to be composed of a thick layer of hyaline material bounded on the exterior by a definite membrane. Possibly by a process of shrinking or infolding, the wall assumes the configuration shown in figure 88.

The composition of the wall has not been definitely determined. It does not stain with either chloro-iodide of zinc or iodine-potassium iodide followed by sulfuric acid. In this respect it is different from that of the evanescent sporangium, which gives a weak reaction for cellulose.

The resting spore appears to be nothing more than an incipient sporangium which has encysted and developed a thick wall in the early stages of development. It is usually uninucleate, figure 87, but occasionally binucleate as in figure 88. The latter may have arisen in one of several ways, but so far I have found no evidence that the binucleate condition

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Explanation of Plate 7

Fig. 101. Unusual resting spore formation within the rhizoid of a resting spore thallus ($\times 865$).

Fig. 102. Initial stage in the germination of a resting spore, showing the dispersion of the refringent mass ($\times 865$).

Fig. 103. Later stage in resting spore germination ($\times 865$).

Fig. 104. Advanced stage in the germination, with the highly refractive globules of the zoospores becoming evident ($\times 865$).

Fig. 105. Mature zoosporangium showing the zoospore initals completely delimited ($\times 865$).

Fig. 106. Empty zoosporangium showing the operculum ($\times 865$).

Fig. 107. A resting spore bearing a sporangium at the end of a long tube ($\times 865$).

Fig. 108. Germinated resting spore in which the sporangium has formed at the end of a long tube showing zoospores germinating *in situ* ($\times 865$).

Fig. 109. Degeneration of protoplasm in tube of germinating resting spore ($\times 865$).

Fig. 110. Germinating resting spore, from fixed and stained material showing the two nuclei in the evanescent zoosporangium ($\times 865$).

Fig. 111. A four nucleate stage of the evanescent sporangium formed by the germinating resting spore.

Fig. 112. Empty zoosporangium of a resting spore extending beyond the wall of the evanescent sporangium in which the resting spore had formed ($\times 865$).
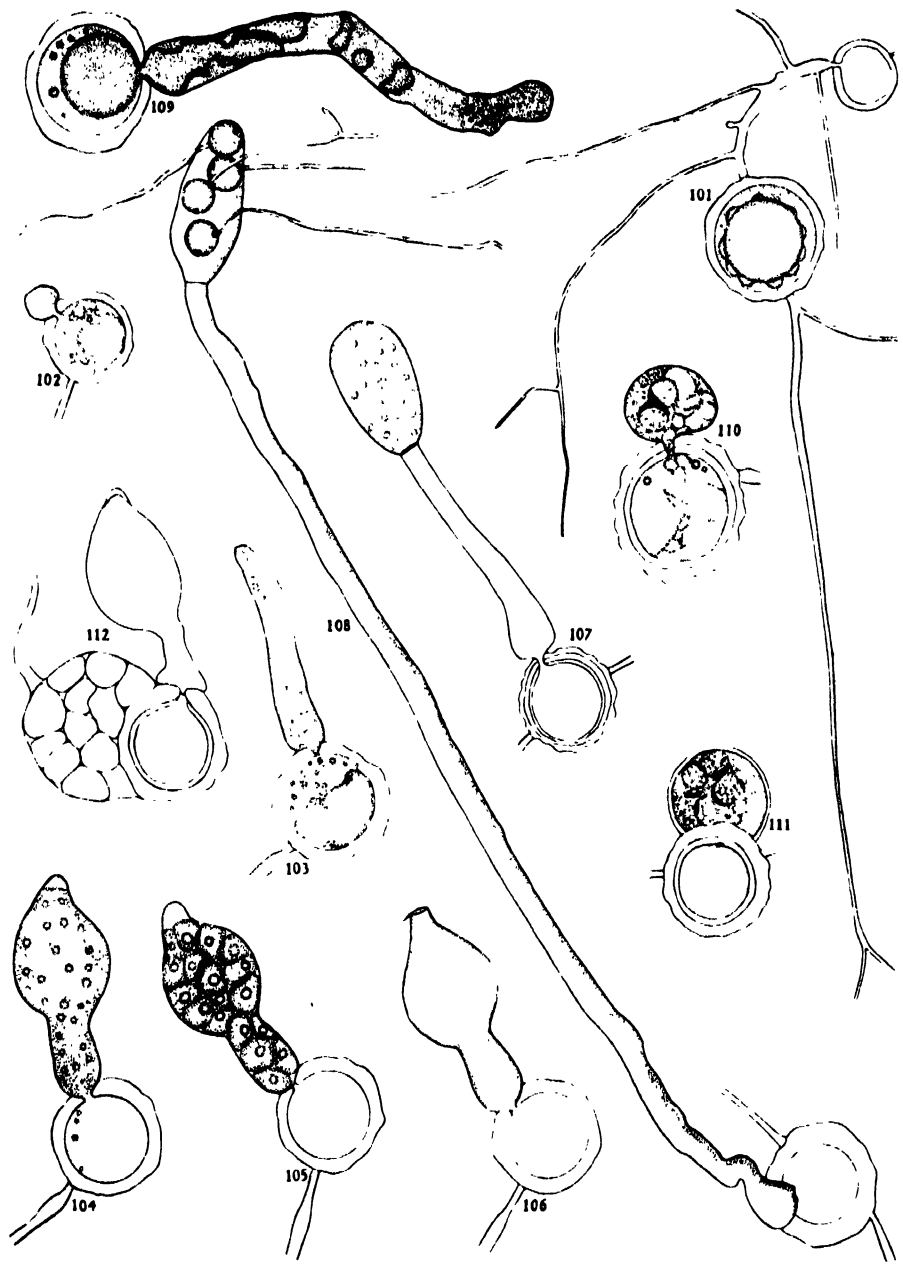
is the result of sexual fusion. Biciliate zoospores which may look like motile biciliate zygotes have been seen, but these have apparently arisen as the result of incomplete cleavage. Instances of two nuclei in the germ tube and in the incipient sporangium have already been shown in figures 28 and 32, and the binucleate resting spores may have arisen from such thalli.

Figure 100 shows an interesting and significant occurrence of three resting spores within an old zoosporangium which apparently has failed to open. Such sporangia containing as many as a dozen resting spores have frequently been found in my material. It is to be particularly noted that there is no evidence of rhizoids, and the resting spores appear as if they had arisen directly by the mere enlargement of a zoospore. If such is the case, it is obvious that *E. operculatum* may occasionally exhibit the same type of monocentric development as the Myxochytridineae. On the other hand, another variation of thallus organization of rather rare occurrence is shown in figure 101 in which polycentricity is exhibited. A smooth walled resting spore has developed nearest the germ tube while a rough walled spore has formed in the rhizoid. The smooth walled spore is empty, which might suggest that the contents had migrated into the rhizoid to establish a second center of reproduction.

Germination of the Resting Spore.—In February, 1938 germinating resting spores of *E. operculatum* were first found in filaments of *Clado-phora* which had previously been cleared in potassium hydroxide. The first step in germination is apparently the formation of a small germ pore in the wall of the spore, and through this aperture extrudes a small vesicle filled with finely granular protoplasm as is shown in figure 102. At the same time the large refractive globule appears to divide into smaller units, figures 102 and 103, and these in turn become finely divided to form small granules. The protoplasm within the spore is homogeneous except for the large, irregular mass which is apparently the residue of the central refringent body. The vesicle that forms upon germination may develop directly into the sporangium, figures 103 to 106, or elongate to form a tube the tip of which is delimited by a cross wall and develops into a sporangium, as is shown in figures 107 and 108. This long tube is evidently an adaptation upon the part of the fungus to discharge its zoospores to the outside of the host cell. The protoplasm in the incipient sporangium is quite uniformly granular. Not many of the stages of germination have been observed in fixed and stained preparations but from the results obtained it appears that mitosis occurs in the sporangium

and not in the resting spore. So far no uninucleate stages of the incipient sporangium have been found, but in figure 110 is shown a binucleate stage. This condition may have arisen by the germination of a binucleate resting spore, such as is shown in figure 88, or by division of the primary nucleus after its migration into the incipient zoosporangium. I am inclined to take the latter viewpoint. That further mitoses occur in the development of the sporangium rather than in the resting spore is suggested by figure 111 which shows a tetra-nucleate stage. The stages which have so far been found correspond closely with those of Wager (1913) for *P. Euglenae.* Figures 104 and 105 show successive stages in the maturation of a fully formed sporangium. The processes of maturation and zoosporogenesis here are very similar to those described for the evanescent primary sporangium. The protoplasm is uniformly granular in the late developmental stages, and then the minute refringent granules appear to coalesce gradually, figure 104, to form the large refractive globule of the zoospore, figure 105. The clear region evident beneath the operculum of the evanescent sporangium, is likewise present in, and characteristic of these sporangia. The cleavage lines in the early stages are difficult to see, but later, as in figure 105, they may be distinguished fairly well. The zoospores are discharged through an operculate opening, figure 106, flow out in a globular mass, and lie quiescent for a short time before becoming active and swimming away. They are in all respects similar to those produced by the evanescent sporangium. In exceptional cases when the operculum fails to push up, the zoospores are discharged at the edge of the operculum, as is shown in figure 112. This figure shows a germinated intra-sporangial resting spore with the new sporangium developed through the wall of the old evanescent sporangium. As has been noted above, the germinating resting spore may sometimes form a long tube, instead of a globular sporangium, which swells up at the tip, as is illustrated in figures 107 and 108. As all or most of the protoplasm has moved up into the swollen tip, it is delimited by a cross wall, in the same manner as De Bary (1884) showed in *Chytridium olla,* and has been transformed into a zoosporangium. Figure 108 shows such a tube which is exceptionally long measuring 134μ. It is also to be noted here that the zoospores formed in the tip failed to emerge and have germinated *in situ.* Quite often resting spore germination may be arrested so that the incipient sporangia degenerate leaving a large amount of refringent material, as in figure 109 which shows a spore having a long tube, but no further development.

The method of resting spore germination described above is fundamentally similar to that reported for most chytrids. The resting spore functions as a cyst or prosporangium and upon germination gives rise to a thin-walled evanescent zoosporangium as in *Rhizidium mycophilum* (Nowakowski, 1877a), *Polyphagus Euglenae* (Nowaskowski, 1877b); (Wager, 1913), *Entophlyctis vaucheriae* (Fisch, 1884), *Chytridium olla* (De Bary, 1884), *Megachytrium Westonii* (Sparrow, 1933), *Chytridium lagenaria* (Karling 1936b), *Diplophlyctis intestina* (Karling 1936a), *Rhizidiopsis Emmanuelensis* (Sparrow 1933, 1936), *Rhizophidium graminis* (Ledingham, 1936) and *Rhizophidium sp.* (Karling, 1939).

The nature of the refringent substance of the zoospores and resting spore.—One of the characteristic features of many chytrid zoospores is the presence of a spherical or oval, highly refractive globule. This substance has many of the properties of oil, and it has been commonly described in the literature as an oil or fat droplet. This body in *Endochytrium* and in most other rhizidiaceous chytrids is usually spherical, and its plastic and viscid nature becomes evident during the amoeboid stages of the zoospores. Its composition is apparently more complex than that of a simple fat or fatty acid and until further specific chemical tests have been made to determine its nature I shall use the descriptive term "highly refractive" or "refringent globule."

As has been noted above, the highly refractive substance occurs most abundantly in the resting spore, forming a large central globule, and several of the common tests for fats and oils have been made on the substance within the spore. By soaking the resting-spore in sodium hypochlorite for two hours the thick walls were dissolved to permit rapid penetration of the reagents and to facilitate observations. There is the possibility that the treatment thus given the resting spores in dissolving the cell walls may have changed the composition of the cell contents, but in each case the results of the tests with the solvents and stains were the same as those of the untreated spores.

The substance in the resting spore is soluble in ether, chloroform, xylol and insoluble in absolute alcohol at room temperature. It reduces osmic acid and is stained by the Sudan III, Sudan IV and Nile blue sulfate, which are specific for fat. Sudan III and IV stain the highly refractive substance yellow to scarlet, and Nile blue sulfate stains the substance either red, blue, or reddish blue thus making it impossible to determine whether the material is a neutral fat or a fatty acid. Sudan stains should give a scarlet red color with fats, but at times a yellow color was obtained. The

highly refractive substance in degenerating protoplasm, such as that shown in the sporangium of figure 109 stains much more rapidly and brilliantly than the substance found in living protoplasm. This, according to Cowdry (1924) may be due to the physiological condition of the organism, the yellow color resulting when staining a living cell and red when the cell is dead. The substance does not give any of the glycogen reactions with either iodine-potassium iodide, Best's carmine method, or by hydrolysis to form sugar.

The fat indicators Sudan III, IV and Nile blue sulfate were applied to the fungus in all stages of its development. The results indicate that the highly refractive substance is present at all times in various stages of dispersion, and particularly abundant in the rhizoids during the developmental stages. In the rhizoids of mature evanescent sporangia it has been observed only in the distal positions which would indicate that most of the highly refractive substance has been transferred to the sporangium.

DISCUSSION

The Chytridiales are not represented by any single type of thallus structure. The simpler forms included in the Myxochytridineae are holocarpic and without absorbing organs. The Rhizidiaceae, on the other hand, are eucarpic with an absorbing organ that varies from a simple unbranched knob, peg, or filament as in *Tylochytrium* to a well-developed and extensive rhizoidal system as in *E. operculatum* and *Rhizophlyctis petersenii*. The Cladochytriaceae, which include more highly developed forms, possess a rhizomycilium with many centers of growth and reproduction. The thallus of the Rhizidiaceae may thus perhaps be regarded as an intermediate type between the nonrhizoidal and rhizomyceloid species. This variation in the structure and complexity of the thallus has suggested many problems dealing with the possible evolutionary tendencies of this group in relation to the origin of the mycelium and the nature of the thallus organization with respect to nuclear distribution. Heretofore, the Rhizidiaceae have been considered largely from the standpoint of sexuality and phylogeny, based mainly upon the study of living material, and few studies have been made on fixed and stained material with respect to the morphology of the thallus.

In this study of *E. operculatum* it has been observed that the nucleus, upon germination of the zoospore, migrates into the incipient sporangium thus transferring the center of growth and reproduction. During the developmental stages, the thallus consists of a single cell which is modified

locally into a vegetative center of growth and a rhizoidal system. Although evidence of flow of protoplasmic material between the rhizoid and the incipient sporangium has been found, nuclei have not been observed in the rhizoids but appear to be localized within the developing sporangium. Nemec (1912) had found that nuclei in the thallus of *Entophlyctis salicornae* were localized in the sporangium but, as far as I am aware this is the only report concerning nuclear distribution in an intramatrical, rhizidiaceous form possessing a well developed rhizoidal system. The localization of the nuclei in the incipient sporangium of *E. operculatum* and their exclusion from the rhizoids precludes the possibility of the reduplication of centers of growth and reproduction within the absorbing system. Karling (1937b) from his study of *Cladochytrium replicatum* concluded that the reduplication of centers of organization was associated with the migration of one of the daughter nuclei following the first division of the primary nucleus in the spindle organ into the rhizomycelium. At this time he suggested that the development of the monocentric type of thallus possessing rhizoids is associated with the localization of nuclei in the sporangium and that additional centers of growth and reproduction are not found since the nuclei do not migrate into or occur in the rhizoids. This investigation of *E. operculatum* tends to support the contention of Karling regarding the nature of thallus organization.

The question of differentiation of the absorbing organ of the Rhizidiaceae from a mycelium, holdfast, rhizomycelium and possibly a rhizoid is yet a matter that must be settled. Zopf (1884), Schroeter (1897) and Fitzpatrick (1930) consider the rhizoids as mycelia, while Fischer (1892), Atkinson (1909), Petersen (1910), and Gauman and Dodge (1928) call them rhizoids. Bessey (1935) uses either rhizoid or haustorium, while Nemec (1912) used the term haustorium. The terminology employed for the vegetative and absorbing organs of the fungi was reviewed by Karling (1932) in which he defined rhizoid as being distinguishable from the mycelium by "their decreasing in diameter from the point of origin and tapering to extreme fineness without any tendency to form new centers for the processes of growth differentiation and reproduction." It is distinguished from the haustorium by its tapering to a fine tip instead of remaining as broad lobes as the haustoria. Its function is different too in that the rhizoid is usually present in saprophytic forms while the haustorium is associated with parasitic species. It appears from the evidence obtained in this study that rhizoids may be further distinguished from the mycelium and rhizomycelium by their lack of nuclei.

It is significant to note here that the nuclear cap in *E. operculatum* is strikingly similar to that found in species of the Blastocladiales, but whether or not this is indicative of relationship is still uncertain. At present the presence of the nuclear cap in the zoospore of the Myxochytridineae described and the references to it in the Rhizidiaceae are rather vague, although it appears to be present in the latter family. The figures of the zoospore of *Polyphagus Euglenae* show that there is a deeply staining mass of material about the nucleus, which Wager (1913) explains as a chromidial mass, and it appears to be much like the nuclear cap in *E. operculatum*. In other species of the family which have been studied to some extent from fixed and stained preparations, namely *Zygorhizidium Willei*, Lowenthal (1905), *Mitochytridium ramosum*, Couch (1935b) and *Rhizophidium Beauchampi*, Hovasse (1936), there is a suggestion of nuclear caps, but the figures and descriptions are as yet insufficient. The nuclear cap is, however, well defined in *Blastocladia Pringsheimii* (Thaxter) (1896), *B. strangulata* (Barrett 1912), B. Pringsheimii and B. Globosa (Cotner 1930a), *Allomyces Javanicus* (Kneip 1929), *A. arbuscula* (Hatch 1935, 1938). Cotner (1930b) shows structures in the gametes of *Apodachlya brachynema, Saprolegnia monoica* var. *glomerata, Achlya conspicua, Aphanomyces euteiches* and *Phytophthora palmivora* which may be nuclear caps, but are less sharply defined than those in the preceding group. The structure of the zoospore has been utilized by Miss Matthews (1937) as a criterion to establish *Blastocladiella*, a new genus, with the Blastocladiales rather than to the Chytridiales although in thallus structure it resembles *Macrochytrium botrydioides* of the Rhizidiaceae more closely. If the zoospore structure of *E. operculatum* is compared with that of other species of the Phycomycetes it becomes evident that outside of the Rhizidaceae it is more closely allied to the *Cladochytrium replicatum* and the Blastocladiales than to the Myxochytridineae.

SUMMARY

The cytology of *E. operculatum* is described in its relation to the development and organization of the thallus, the formation of the evanescent sporangium, and the development and germination of the resting spore.

The zoospore possesses an extra-nuclear cap which appears to vary greatly in form and in its staining reactions. The origin and function of the cap have not been determined.

Upon germination the zoospore produces a filamentous branched or unbranched germ tube, into which the nucleus migrates. The latter comes to rest in a swollen portion of the germ tube which becomes the new center of organization of the thallus. The distal portions of the germ tube give rise to the rhizoidal system.

The nucleus following its arrival in the rudiment of the sporangium enlarges, probably doubling its size before division occurs. Subsequently enlargement of the sporangium is accompanied by nuclear division.

Nuclear division in the primary evanescent sporangium is mitotic and simultaneous. The spindle is intra-nuclear with central bodies at the poles which appear to be extended through the nuclear membrane during the anaphases. Astral rays have been found to radiate from the central bodies of some nuclei. Cleavage of the protoplast to form the uninucleate zoospores is by progressive furrowing.

The development of the resting spore is similar to that of the evanescent sporangium up to a certain stage, but they develop a thick, rough or smooth wall which appears to be composed of three layers. The protoplast is displaced to the wall of the resting spore as a thin peripheral layer by the large highly refractive globule that occupies the center of the cell. The spore, usually uninucleate, may occasionally be bi-nucleate.

The resting spore functions as a prosporangium and upon germination develops an operculate evanescent sporangium on its surface or at the end of a long tube.

The center of growth of the *E. operculatum* is transferred from the zoospore to some position in the germ tube which then becomes the zoosporangium. The thallus is monocentric and this type of organization appears to be associated with the localization of nuclei in the zoosporangium and their exclusion from the rhizoids.

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Stem Morphogenesis in Lycopersicum: A Quantitative Study of Cell Size and Number in the Tomato

HELEN B. HOUGHTALING

(WITH PLATE 8 AND TEN FIGURES)

In a typical dicotyledenous herbaceous plant, the stem increases in length as the result of the activity of a group of meristematic cells situated at its tip. By these cells the primary tissues are laid down and the fundamental anatomical arrangement of the stem is determined. For several internodes below this meristem, growth takes place in the primary tissues at different rates with the result that the relative sizes of the tissues are changed (Sinnott, 1936). Thus the anatomical pattern is altered. The purpose of this study is to determine what changes take place in the development of the stem in several varieties of *Lycopersicum esculentum* and one variety of *L. pimpinellifolium*, and to discover the mechanism through which the differences in stem size which exist in these types and their hybrids become established.

One of Mendel's original seven characters in peas was concerned with length of stem. Dwarf plants were recessive to tall, and segregated in the F_2 in the ratio of one dwarf to three tall. The inheritance of height in peas was found to be more complicated by Keeble and Pellew (1910) who found two factor pairs concerned with length and thickness of stem respectively. These combined to make a very tall plant. The double recessive produced an extreme dwarf type, and either factor alone produced a plant which was intermediate between the two extremes. Numerous examples of genetic control of height in plants might be cited. In tomatoes the dwarf habit of growth is recessive to the tall, and is controlled by a single pair of Mendelian factors. Thus we have direct evidence that length of stem and height of plant are genetically controlled not only in other plants but in the tomato itself.

The work of Sinnott, Blakeslee and Houghtaling (1934) on *Datura* peduncles offers an excellent example of the anatomical structure of the plant being subject to genetic control. In this genus the presence of an extra chromosome affects both anatomical structure and cell size. Except within the polyploid series, there is little evidence for a necessary relationship between anatomical pattern and size of stem. Large stems may be large through increase in number of cells or through increase in size of cells. Sometimes vascular tissue may be increased without the increase necessarily being accompanied by any other structural enlargement.

However, work on *Datura* was all done at the midpoint of the flower peduncle on the day of flowering. Work has been done on the developmental relationship of cell size to fruit size (Houghtaling, 1935; Sinnott, 1939), and it has been found that, in general, a period of cell division with perhaps some increase in cell size is followed by a period of cell enlargement with no further division. This present study deals with cell and tissue relationships in the development of the main stem of the tomato.

MATERIAL AND METHODS

The material used was derived from three pure lines of *Lycopersicum esculentum*, "Bonnie Best," "Red Cherry," and "Dwarf Champion," and one pure line of *L. pimpinellifolium*, "Red Currant." These had all been inbred through five to eight generations and showed no recognizable genetical variability. Crosses were made between Bonnie Best and Red Cherry, Bonnie Best and Red Currant, and Dwarf Champion and Red Currant. One F_2 of one hundred plants was grown from the F_1 of the cross Bonnie Best by Red Currant. All these plants were grown in the University of Michigan Botanical Gardens during the summer of 1935. More were grown in 1936 and 1937, but the material studied was largely taken from the plants raised in 1935. The photographs (plate 8) were taken in 1937, but comparable measurements showed that these plants were essentially similar to those raised in 1935.

These particular types were chosen for study because they were characterized by large differences in thickness of stem (plate 8). The difference between *L. pimpinellifolium* and *L. esculentum* is, as might be expected, the greatest. Although the various types of *L. esculentum* are vegetatively · very similar, still an obvious difference exists between Bonnie Best and Dwarf Champion.

Certain gross measurements were made in the field. Stem and internode length were measured with a ruler, and diameters were measured by micrometer calipers. For all length measurements the meristem was taken as the point of reference. A few mature fruits were measured from

Explanation of Plate 8
Branches from typical plants

1 = Bonnie Best	4 = Dwarf Champion
2 = Red Cherry	5 = Red Cherry × Bonnie Best
3 = Red Currant	6 = Dwarf Champion × Red Currant

HOUGHTALING: STEM MORPHOGENESIS

every plant. The fruits were cut along a polar axis, and the polar and equatorial diameters were measured with a ruler.

For anatomical study, transverse and longitudinal hand sections were made along the stem at various distances from the meristem. These were stained in safranin and mounted for study in glycerin. For more careful study, material was fixed in seventy percent alcohol, with five percent
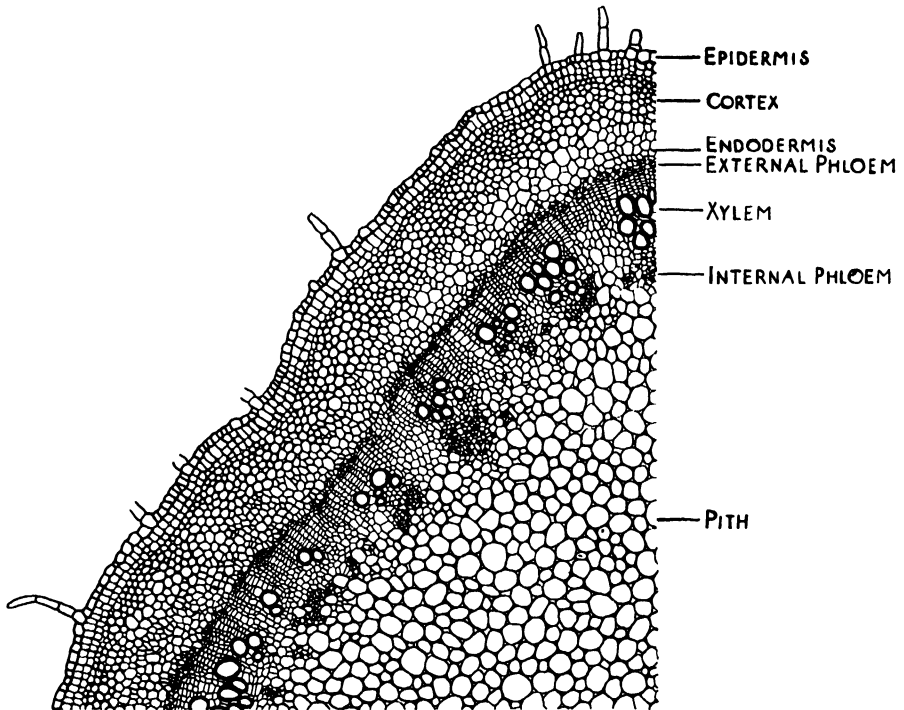
Fig. 1. Diagram of a portion of tranverse section through a stem of Bonnie Best showing tissues studied.

acetic acid and five percent formalin added, then imbedded in paraffin, sectioned with a rotary microtome ten to fifty micra thick, and stained in Delafield's haematoxylin and safranin.

The anatomy of the typical tomato stem has been described by Woodcock (1936). Externally the stem is protected by a single epidermal layer (fig. 1). Underneath this is a hypodermal layer which in young stems is one cell thick. This single layer of cells apparently divides, forming two or three layers in older stems. The outermost cells frequently elongate radially. These cells contain chloroplasts. Beneath the hypodermis there is a region of parenchymatous cells which form

the major part of the cortex. An endodermal layer is marked by the presence of starch grains when fresh material is stained with iodine. Woodcock was able to discern Casparian strips, but the author could find none in this material. The cross section of the vascular bundle shows both internal and external phloem, lying in patches on either side of the xylem. The cambium is easily visible, and in older stems considerable secondary growth is evident. Within the ring of vascular tissue lies the pith made up of large parenchymatous cells.

Anatomical measurements were made in various ways, some with a micrometer eyepiece in the ordinary compound microscope, but the majority with a projection apparatus. The sections were put in the machine, the magnified image was projected on paper and drawn, and measurements were made on the drawings. Various magnifications were used, care being exercised that all measurements of a given kind were made at the same time. In measuring cells the ten largest were chosen from each tissue. This was done to avoid those which were not cut through the equatorial diameter and to standardize procedure as much as possible. Ten cells were measured from typical regions of the epidermis, cortex, and pith. In cortical and pith cells, two diameters of each cell were measured at right angles to one another and averaged. The average was recorded as representing the diameter of the cell.

To calculate the cross-sectional area of the cell, this diameter was squared and multiplied by the factor $\Pi/4m,^2$ where m denotes the magnification. This gave the area of a circle with the original diameter. Thus it was possible to correct for shape and magnification with a single mathematical operation. Since the epidermal cells were not circular in shape it was necessary to multiply the two diameters obtained in the original measurements together to obtain the area of a rectangle and then correct for magnification. These figures, circle and rectangle, closely approximate the actual shape, and hence also the area, of the cells concerned. Further, since the variations from these fundamental figures are at random within a tissue, these calculations may safely be used for the purpose of comparison.

To find a representative cell size for each tissue, the geometric mean of the area of the ten cells measured was calculated. The reason for using geometric means rather than ordinary (i.e., arithmetic) averages lies in the fact that these measurements are of growing cells and growth is a geometric process. Likewise, by the method of computation of cross-sectional areas which was used, the geometric mean was more easily

obtained. In any case the geometric mean differs only slightly from the arithmetic mean and seems to give a more accurate picture of size changes.

Tissue measurements were made from the same sections in which cell size was studied. The stem was projected at a lower magnification and drawn. A line was drawn at the outer limit of the epidermis, one at the outer limit of the external phloem, and one at the inner limit of the internal phloem. Two diameters of each were measured. The area of each was calculated from the average diameter in the same manner as area of pith cells was found. From these areas the cross-sectional area of the stem, cortex, vascular cylinder, and pith were computed.

Fig. 2. Diameter of stem plotted logarithmically against distance from the meristem. Each curve represents approximately 100 measurements.

4 = Dwarf Champion
4 × 3 = Dwarf Champion × Red Currant
1 × 3 = Bonnie Best × Red Currant

1 = Bonnie Best

RESULTS

The differences in diameter of stem and length of internodes are shown in the photographs (plate 8). Measurements show that at equal distances from the stem tip these various tomato varieties have marked differences in diameter. Figure 2 shows the diameter of the stem measured at the mid-point of the internode plotted logarithmically against the distance of that point from the tip of the stem. In the pure lines the difference in stem diameter is already established at one centimeter from the tip. Measurements with calipers were not very accurate within a distance of one centimeter from the tip because of the proximity of young leaves. However,

examination of microscope sections shows that the differences in stem size continue back into the meristem itself. The curves in figure 2 show that the differences which are established so early are maintained throughout the growth of the stem. For example, at one centimeter from the tip the stem diameter of Bonnie Best is a little less than twice that of Red Currant, at five centimeters from the tip the former is still just a little less than double the latter, and at ten centimeters the same relationship holds. In other words, relative increase in stem diameter takes place at the same rate with respect to distance from the meristem in both types. Figure 2 shows that this is true for all the types studied. The tendency for the cures to flatten between ten and twenty centimeters from the tip is undoubtedly because of the termination of increase in diameter by primary growth with the assumption of secondary growth. The hybrid, Bonnie Best × Red Currant, lies between its two parents, rather nearer Red Currant.

Table 1 gives the average diameters of the stems at five and ten centimeters from the tip. For the hybrids, the arithmetic and geometric means of the parents are given for comparison with the attained values. It is obvious that the hybrids lie very close to the geometric means. The fact that the values obtained from the measurements are slightly smaller in all

TABLE 1

Diameters of Stems

LINE	DIAMETER 5 CMS. FROM TIP	DIAMETER 10 CMS. FROM TIP
RED CURRANT	.187	.250
BONNIE BEST	.350	.450
DWARF CHAMPION	.595	.800
BONNIE BEST × RED CURRANT	.240	.325
Arithmetic mean	.265	.350
Geometric mean	.256	.335
DWARF CHAMPION × RED CURRANT	.300	.425
Arithmetic mean	.386	.525
Geometric mean	.324	.447

instances suggests partial dominance of the smaller parent. The slightly steeper slope of the hybrid, Dwarf Champion × Red Currant, indicating more rapid relative increase in stem diameter, may be the result of hybrid vigor, although there is no indication of the same effect in the other hybrid.

In the course of this work the author noted that in the F_2 population, in which there was complicated segregation of fruit size (fig. 3), the plants
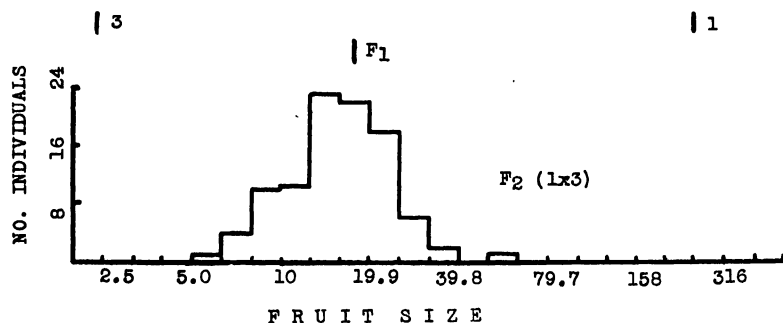
Fig. 3. Diagram shows distribution of fruit size on a logarithmic scale in the F_2 from a cross of Bonnie Best × Red Currant. The positions of the mean value of fruit size in the parents and F_1 are indicated by vertical lines.

with the thicker stems bore larger fruits than those with thinner stems. In the parental types this relation is fairly obvious. The stem diameter of Red Currant at ten centimeters from the tip is .250 cms., and the fruit
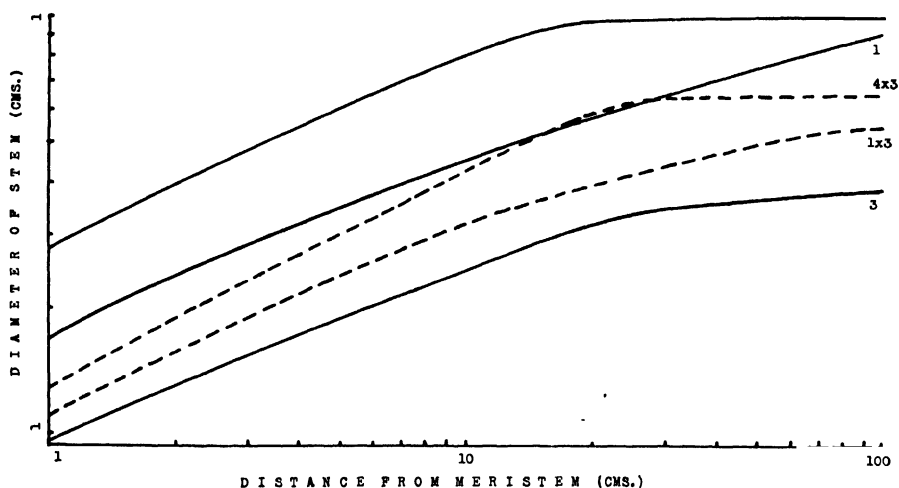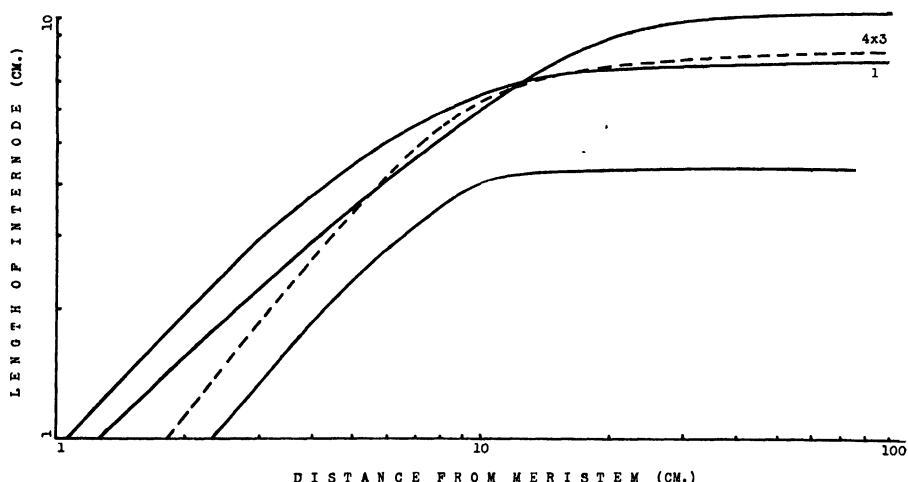

Fig. 4. Length of internodes plotted logarithmically against distance from the meristem. Each curve represents approximately 100 measurements.

3 = Red Currant   1 = Bonnie Best
4 = Dwarf Champion
4× 3 = Dwarf Champion × Red Currant

volume is about 1.5 cu. cm. The corresponding figures for Bonnie Best are .450 cm. for the diameter at ten centimeters and 275 cu. cm. In the F_2 from the cross Bonnie Best × Red Currant, a correlation of .57 ± .03

was found between size of fruit and diameter of stem measured ten centi-
meters from the meristem. This relation may, of course, be the result of
genetic linkage between factors controlling stem and fruit size. It may
also be physiological in that small-stemmed types may be unable to bear
large fruits. However, since the diameter of the stem is determined in the
meristem and Houghtaling (1935) has shown that the size of the fruit
is also determined in the fruit meristem, it is suggested that a morpho-
logical correlation may exist between the meristems of the plant.

The illustrations (plate 8) indicate little difference in internode length
except in Dwarf Champion. Statistical data show that this length is
subject to great variability. There seem to be no or only slight differences
existing among all the types with the exception of Dwarf Champion (fig.
4). In the latter the internodes are relatively shorter than in the other
varieties, not only at first but throughout development so that the relative
internode length is maintained. It seems rather surprising that with the
great difference in diameter that exists between Bonnie Best and Red
Currant there should be practically no difference in length of internodes.
The factors which control diameter have no influence upon length.

Another point of some interest which appeared in measuring inter-
node length is the fact that the internode below a branch is generally
shorter than the internode above the branch although the latter is, of
course, the younger. This is particularly noticeable in the thick-stemmed
types. For example, in Bonnie Best the internode below a branch averages
67 percent as large as the internode above the branch; in Dwarf Cham-
pion, 79 percent; in Red Cherry, 88 percent; and in Red Currant, 89 per-
cent.

In figure 5 the relation is shown between cross-sectional area of the
tissues in the stem and the area of the stem. The distances between the
lines indicate the differences in cross-sectional area of a single tissue in
the several varieties. The slope of the lines indicate the relative rate of
growth of the tissues with respect to stem area, or, more simply, the value
of Huxley's constant, "k" (Huxley, 1932).

For the pith the slope of the lines, or "k," is always unity, which in-
dicates that the area of the pith increases at the same rate as the area of
the stem. In other words, the area of the pith occupies the same proportion
of the stem throughout development. The differences in position of the
lines show that relatively more of the stem is made up of pith in Dwarf
Champion than in Bonnie Best, and more in Bonnie Best than in Red
Currant. The hybrid between these last two lies intermediate between them.

The fact that these lines do not converge at the base indicates that the differences in size of pith are initial differences determined in the meristem and maintained as such through development. It is interesting to note (cf. table 2) that the area of the pith in the types with larger stems is proportionately greater than in those with smaller stems.

For cross-sectional area of vascular tissue the story is not quite so simple. The slopes of the lines are different, being greater for Red Currant than for Bonnie Best, with the hybrid lying between. Dwarf Champion has the least slope of all. This is, of course, in the reverse order of stem size. There is a tendency for the lines to converge at the base. Thus if Dwarf Champion ever produced a stem as small as the smallest studied of Red Currant it would have approximately the same amount of vascular tissue. However, the rate of increase of vascular tissue in Red Currant is much greater than in Dwarf Champion with the result that ultimately the small-stemmed type has a much larger proportion of vascular tissue. The rate of increase of cross-sectional area of vascular tissue with refer-

TABLE 2

Cross sectional areas of Stems and Huxley's Constant, k

LINE	CROSS-SECTIONAL AREA OF STEM AT 10 CMS.	PERCENT PITH	K VASC. CYL. AND STEM	K CORTEX AND STEM
RED CURRANT	.0492	30	1.26	.77
BONNIE BEST	.1580	40.5	1.10	.84
DWARF CHAMPION	.5120	49	1.05	.87
BONNIE BEST × RED CURRANT	.0860	39	1.14	.80

ence to cross-sectional area of the stem is inversely proportional to the typical stem thickness of the varieties studied (table 2).

In the pith the slope of the lines for all types is 1. In the vascular cylinder the slope, or "k," is always greater than 1. The area of the vascular tissue in the cross-section increases faster than the stem as a whole. Therefore the cortex cannot increase as fast as the area of the

Explanation of Figure 5

Fig. 5. Cross-sectional area of cortex, vascular cylinder, and pith plotted logarithmically against cross-sectional area of stem.

	NO. OF SECTIONS
1 = Bonnie Best	32
4 = Dwarf Champion	17
3 = Red Currant	34
1 × 3 = Bonnie Best × Red Currant	23

The curve showing the relation of the cortex to the stem area for the hybrid was omitted because it lay too close to the curve for Red Currant to show distinctly.
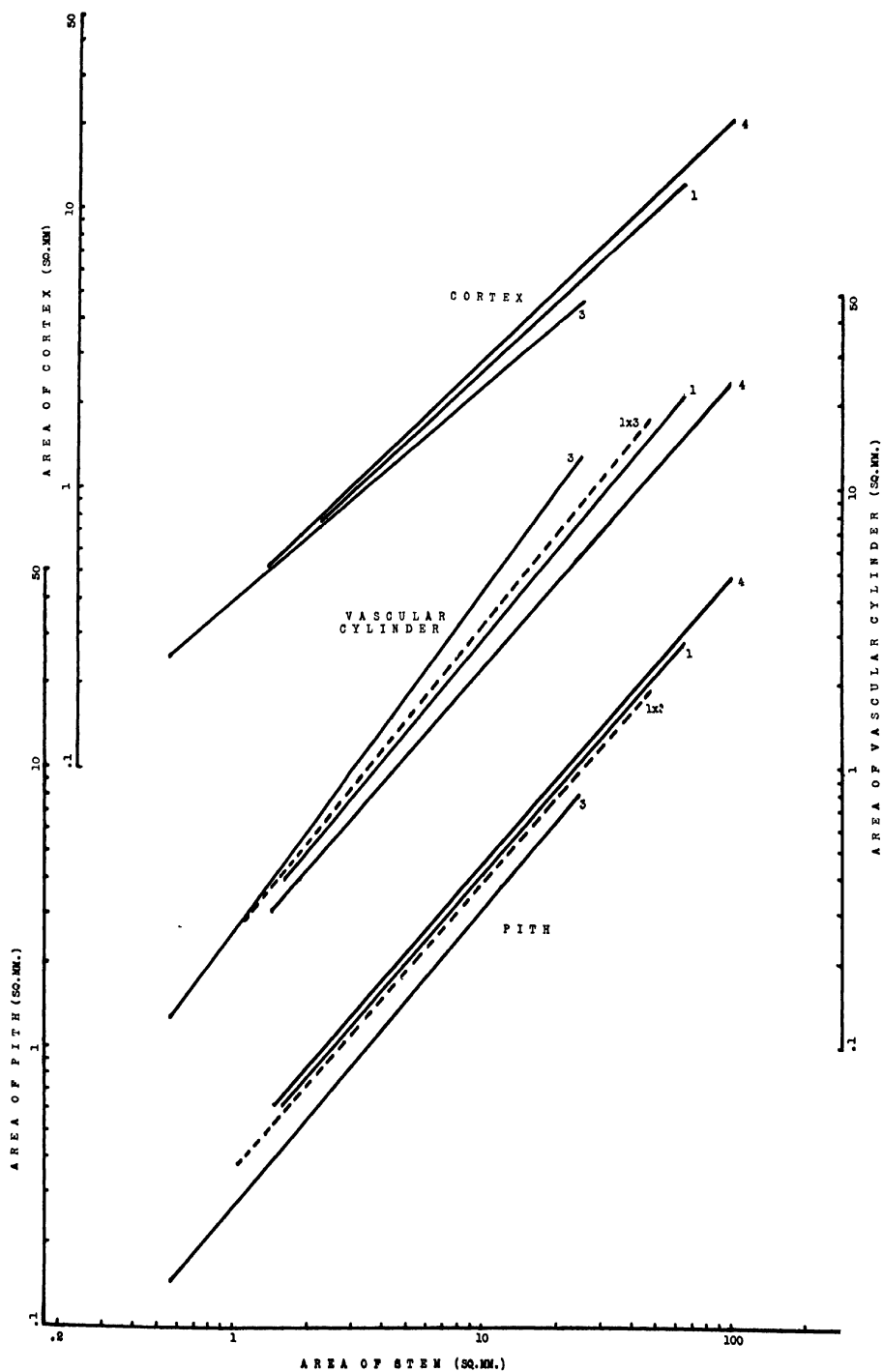
Figure 5

stem. Also since the greatest rate of increase of vascular tissue is found in Red Currant, it is obvious that the slowest rate of increase in the cortex must be found in Red Currant. The lines in figure 5 and the values of "k" for relative rate of increase of cortex with respect to stem in table 2 show that this expectation is fulfilled. Whereas the rate of increase of
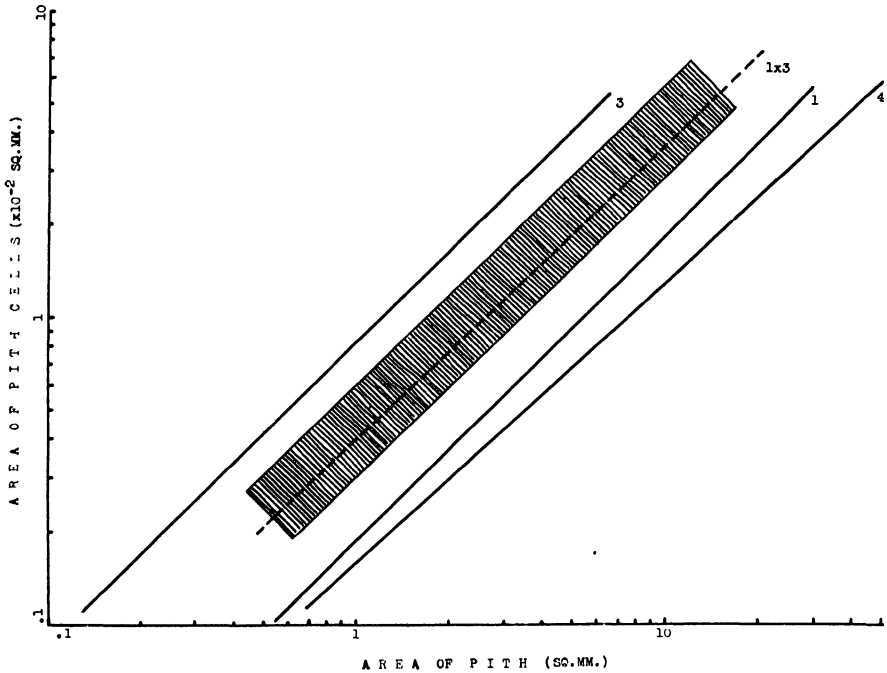
Fig. 6. Cross-sectional area of pith cells plotted logarithmically against cross-sectional area of pith. The shaded area shows the range of the F_2 curves.

	NO. OF CELLS MEASURED
4 = Dwarf Champion	170
1 = Bonnie Best	320
3 = Red Currant	340
1 × 3 = Bonnie Best × Red Currant	170

vascular tissue increases inversely with the stem size of the various types, the rate of increase of cortical tissue varies directly with the stem size.

Cell size was compared with tissue size. Figure 6 shows the relation between cross-sectional area of pith cells with cross-sectional area of pith. The slope of the lines, or "k," is approximately 1, and the cells increase in cross-sectional area at the same rate as the pith. Evidently cell division has stopped and increase in pith area is accomplished by increase in cell size. This is true in all types studied. However, for a pith of given size,

large differences in cell size appear. Red Currant, the smallest-stemmed type, has the largest pith cells. Dwarf Champion, the largest-stemmed type, has the smallest cells, and the other kinds are intermediate in order of their stem size. Figure 7 shows that the same condition holds for cortical cells. The differences in cell size, both initial and ultimate, are smaller than in the pith, however.
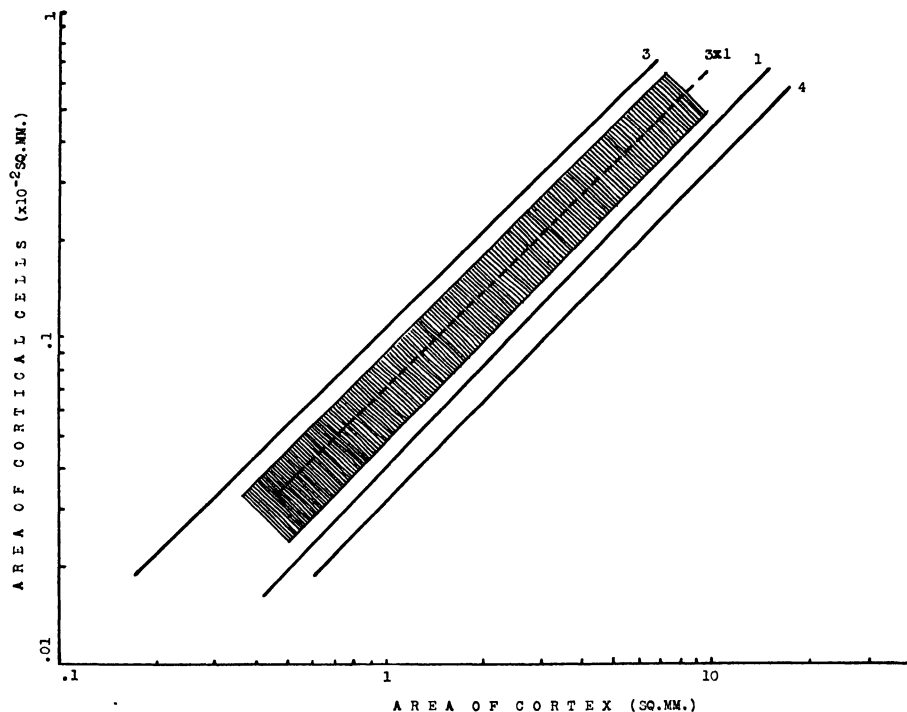
Fig. 7. Cross-sectional area of cortical cells plotted logarithmically against cross-sectional area of cortex. The shaded area shows the range of the F_2 curves.

		NO. OF CELLS MEASURED
4 = Dwarf Champion	....	170
1 = Bonnie Best	....	320
3 = Red Currant	....	340
1 × 3 = Bonnie Best × Red Currant	....	230

The cross-sectional area of the epidermal cells is compared with the cross-sectional area of the stem (fig. 8). This relation is probably not a causal one, but it does indicate that the size of the cells does not increase as rapidly at first as the size of the stems, which means that for some time cell division continues to occur. Later the slope of the curve does approach 1, at which time cell division has stopped. It has long been known (Brotherton and Bartlett, 1918; Sinnott, 1930) that cell division may persist

longer in the epidermal cells than in the other primary tissues. Most interesting is the fact that the order of the curves shows that the same relative cell size and tissue or stem relationship holds here that exists in the other tissues. Red Currant, the smallest-stemmed type, has comparatively the largest cells in all tissues, with the hybrid Bonnie Best $\times$ Red Currant next, then Bonnie Best, and finally Dwarf Champion. Thus the larger the stem of a variety, the smaller its cells are with respect to those of the other varieties.
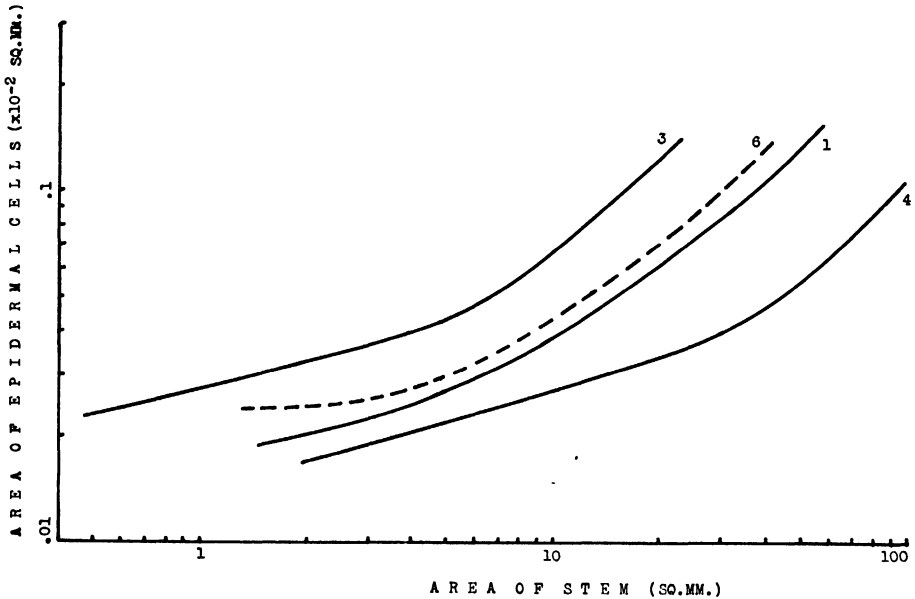
Fig. 8. Cross-sectional area of epidermal cells plotted logarithmically against cross-sectional area of stem. The number of cells measured for each curve varies from 170 to 370.

3 = Red Currant   4 = Dwarf Champion
1 = Bonnie Best   6 = Dwarf Champion $\times$ Red Currant

In a pith with cross-sectional area of one square millimeter, Red Currant will have much larger cells than Bonnie Best will have in pith of equal size. But Bonnie Best starts development with a much larger pith than Red Currant and therefore pith area of one square millimeter will be found in much younger stem of Bonnie Best than in Red Currant. Thus the possibility of a relationship between cell size and age, or, perhaps more suitably, degree of maturation, is suggested. The degree of maturation, a function of time, can be obtained only through some indirect measurement. The measure which suggested itself was the distance from the

meristem. Figure 9 shows the relation to distance from the meristem of stem diameter, pith diameter, thickness of vascular tissue, and diameter of pith cells, for one individual stem from a plant each of Red Currant and Bonnie Best. These are all plotted on a logarithmic scale to the base
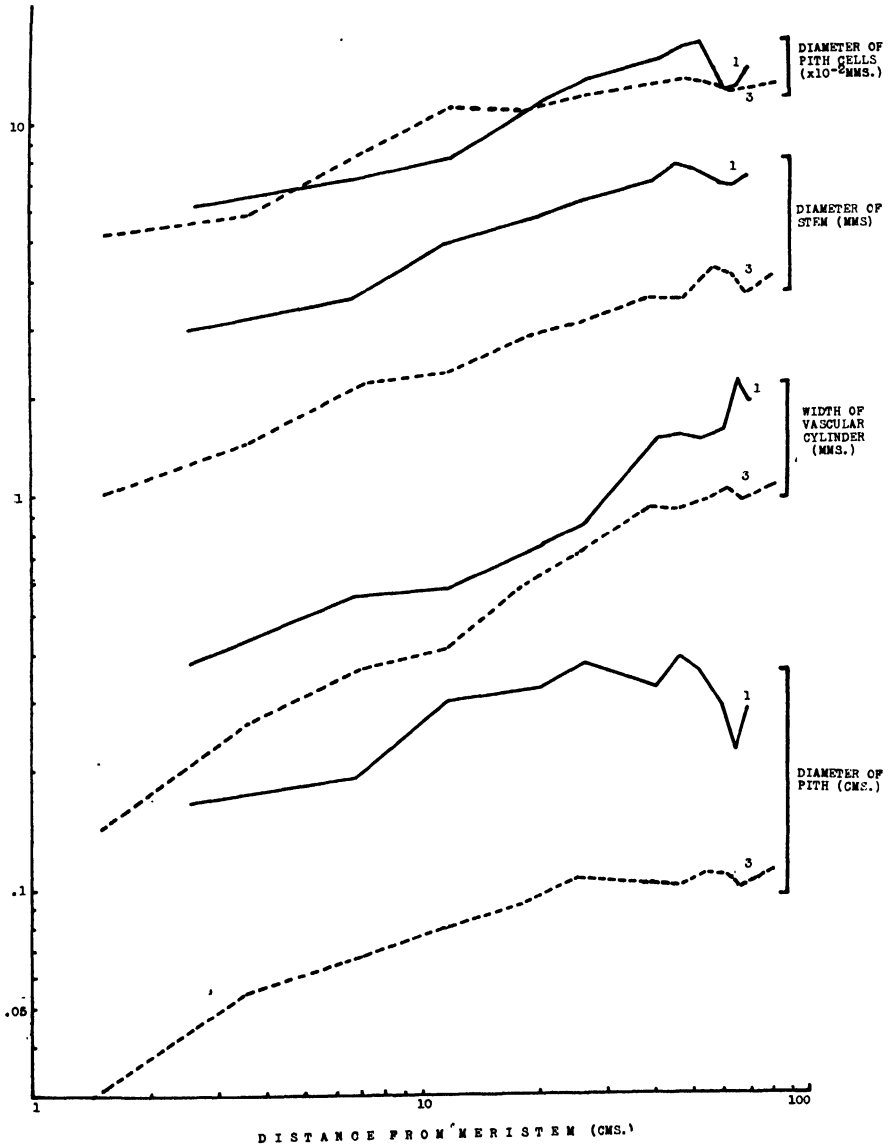
Fig. 9. Diameter of pith cells, stem, pith, and width of vascular tissue plotted logarithmically against distance from meristem.

1 = Bonnie Best   3 = Red Currant

ten with equal intervals representing the multiple ten (as, for instance, those from 1 to 10 and from 10 to 100, respectively). Thus the distances between the curves for Bonnie Best and Red Currant for stem diameter may be compared directly with the distances between the curves for pith cells.

With this in mind it is obvious from the figure that although great differences in size of pith exist, there is no difference in pith cell size among the varieties with long internodes if distance from the meristem is the same. Also, the size of cortical cells is exactly parallel, and is strictly a function of distance from the meristem. This is further brought out in table 3 where cell size is given at various intervals down the stem. There is very close agreement for Bonnie Best, Red Currant, and their hybrid.

TABLE 3

Cross-sectional Area of Cells

| | DISTANCE FROM MERISTEM | | | | | | | |
| | 1 cm. | | 2.5 cm. | | 5 cm. | | 10 cm. | |
LINE	Pith	Cortex	Pith	Cortex	Pith	Cortex	Pith	Cortex
BONNIE BEST	.160	.0295	.39	.062	.71	.104	1.20	.167
RED CURRANT	.165	.0359	.37	.062	.74	.103	1.27	.162
BONNIE BEST × RED CURRANT..	.180	.0375	.37	.060	.88	.100	1.32	.165
DWARF CHAMPION	.485	.0620	1.12	.137	1.95	.270	3.60	.400

Bonnie Best and Red Currant are classified as belonging to different species; the former, *Lycopersicum esculentum,* and the latter, *L. pimpinellifolium.* Lindstrom and Humphrey (1933) found that *L. pimpinellifolium* has smaller chromosomes (although the number is the same) than *L. esculentum.* Navashin (1931) working on *Crepis* found a direct relation between amount of chromosomal material and cell size in the meristem. In these two species of tomato, cells were measured in longitudinal sections of the meristem with an eyepiece micrometer and no difference was found in area. The method of making measurements was not as accurate as that employed by Navashin, and it is possible that a more refined technique would show differences. However, in view of the results in older tissues, differences do not seem probable.

From table 3 it is apparent that the cells in the pith (or in the cortex) of Bonnie Best and Red Currant and their hybrid agree almost exactly in size at equal distances from the tip of the stem. This is not true in Dwarf Champion in which the cells are very much larger. In Bonnie Best and

Red Currant internode length was the same, but in Dwarf Champion the internodes were shorter. It was thought that perhaps at an equivalent number of internodes from the tip cell size in Dwarf Champion would be the same as in the other types. In making measurements the number of internodes was not counted. However, since it was known that the internodes in Bonnie Best are approximately twice as long as in Dwarf Champion, it might be assumed that at 2.5 centimeters from the tip Dwarf Champion would have as many internodes as Bonnie Best at 5 centimeters from the tip, etc. It is obvious from the table that the cells in Dwarf Champion are still much larger than would be expected on this assumption. However, length from the tip in the morphologically similar varieties and their hybrid was conceived to be an indirect measure of a time interval, and there is no evidence that number of internodes in morphologically different varieties can be treated as a measure of time any more than distance from the meristem.

It has already been pointed out that cell size in the pith and in the cortex, as measured by cross-section, increased at the same rate as tissue. This would indicate that no cell division occurred in these tissues below the meristem. In order to check this conclusion, the cross-sectional area of the tissue was divided by the area of the cells and thus cell number was computed. Although there was considerable variability within each variety, there was no evidence that such variability was not completely at random. Attempts to correlate cell number with tissue cross-section within a variety showed that no relation existed at all and the conclusion was definitely reached that cell number within a variety does not increase below the meristem.

The individual plants of the F_2 from the cross Bonnie Best $\times$ Red Currant were examined developmentally in the same way that the parents were. Fundamentally the same relations held. Cell cross-section increased at the same rate that tissue cross-section did, etc. The group of curves (See figs. 6 and 7), each representing a single individual, fell between the curves for the parents. As might be expected they showed a wider spread than equivalent curves for the parents or F_1, indicating greater variability and thus, as usually interpreted, multiple factor inheritance. There was no clear-cut segregation. These curves were rather difficult to deal with inasmuch as the variability in one individual frequently threw it into the size class of individuals on either side. A large number of measurements would be necessary to locate the curves accurately, and the additional information which would be obtained did not seem sufficient to war-

rant the effort. However, since cell number is fairly constant in the various cross-sections of the individual, it offered a fairly simple means of comparing parents and offspring for that characteristic. The results are given in figure 10 and in greater detail in table 4.

TABLE 4

Comparison of Cell Numbers of Parents and Offspring

		PITH CELLS		CORTICAL CELLS		NUMBER OF CELLS MEASURED
		Number	Standard deviation	Number	Standard deviation	
PURE LINES	BONNIE BEST	563	34	2430	162	320
	RED CHERRY	450	20	2070	169	370
	RED CURRANT	127	5	1045	66	340
	DWARF CHAMPION	664	40	2910	107	170
F_1	RED CHERRY × BONNIE BEST	425	30	1725	128	200
	BONNIE BEST × RED CURRANT	248	14	1410	67	230
	1	187	13	1060	88	
	3	193	12	1210	121	
	5	149	10	1160	106	
	6	187	15	1290	93	
	9	146	8	1210	121	
	13	219	15	1530	218	
	14	178	15	1260	87	
	15	165	13	943	124	120
F_2:	16	252	18	1690	191	to
	17	198	9	1210	104	200
BONNIE BEST ×	18	203	17	1020	77	from
RED CURRANT	19	204	17	1205	205	each
	20	213	16	1050	72	plant
	64	304	36	1970	163	
	67	220	17	1210	171	
	68	219	9	1405	136	
	69	280	11	1820	75	
	70	219	14	1585	169	
	71	323	22	2060	280	
	72	262	14	1680	139	
	73	345	21	2105	160	

Standard errors are given in the table for the calculated values of cell number for each plant. It is obvious that real differences in cell number exist in both cortex and pith. Also it appears that cell number in the cortex is related to cell number in the pith. The value of the correlation is .653 ± .125. Further, within the F_2, cell number in the pith was related to the diameter of the stem at a distance of ten centimeters from the meristem. The value of the correlation was found to be .587 ± .182, in-

dicating that stem size and cell number are related. This relation also holds in the parents. Although in this F_2 the relation may be due to genetic linkage, it seems more plausible to assume that it is a structural necessity, and that the larger stems are larger through the possession of more cells than the smaller. This is of particular interest since it indicates that genetic differences may depend directly upon cell number.

<div align="center">DISCUSSION</div>

Sinnott (1936) studied the relations between the primary tissues in a series of young shoots from a tree of *Pinus Strobus*, in a group of flower stalks of *Datura Stramonium*, and in a series of steles of the fern *Todea*
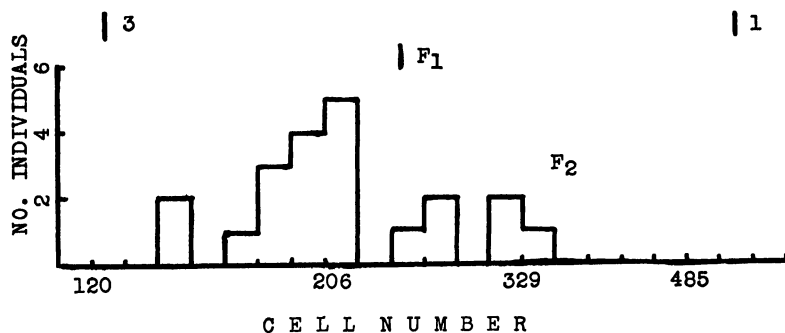
Fig. 10. Diagram shows the distribution of pith cell number in the F_2 of the cross between Bonnie Best and Red Currant. The positions of the mean values of the parents are indicated by vertical lines.

hymenophylloides. Considerable differences in stem size existed within these groups. He found in all of these that the diameter of the pith increased very much faster than the diameter of the stem, the diameter of the vascular cylinder slightly faster or at the same rate as the stem, and the diameter of the cortex very much more slowly than the diameter of the stem. He suggested several possible explanations for the position of the vascular cylinder; first, that it was determined by the position of the leaf primordia; then, that the vascular cylinder may be differentiated at the place where the two different growth rates of pith and cortex come together in the meristem; and lastly, that it is a matter of genetically determined pattern. He says (page 421), "No simple physiological explanation presents itself for these changes in relative size with increasing absolute size. This may be an expression of a developmental pattern inherent in the constitution of the organism."

Buchholz (1938) examined the relationships of tissue size in stems of different dimensions collected from branches of old trees of *Sequoia gigantea*. He found that diameter of stele, diameter of wood cylinder, and diameter of pith plotted against diameter of stem gave a value for "k" of 1.7. Thus pith and vascular tissue were growing at the same rate and very much faster than the stem. Although no figures are given for the cortical tissue it must have grown much more slowly than the stem. He also examined stems which bore male and female cones. The diameter of the stems bearing female cones was very much greater than those bearing male cones. In both, the cone-bearing branches had a relatively smaller pith and larger vascular cylinder than comparable vegetative stems. He found that large stem tips have broader promeristem points with many more cells than those of small stem tips. He presents a very interesting diagram of the promeristems from which the stems of the various types and sizes must have originated. He places all size differences as having their origin in the promeristem.

The two papers just cited both deal with stems which differ in size but not in age. This present paper, on the other hand, deals with size differences which at different levels within the individual plant are correlated with differences in age. Individual plants within a "pure" (i.e., inbred) line are so nearly identical that parts of one may be substituted for exactly corresponding parts of another. The differences among the "pure" lines themselves (the inbred varieties) and among the individual plants of the F_2 are, of course, genetic in origin. That it is possible to prove striking similiarities has been shown in the discussion of cell size in Bonnie Best and Red Currant, whereas extremely different cell and tissue relations were exemplified by the contrast between the two aforementioned varieties and Dwarf Champion.

The developmental study gives results which are not entirely in accordance with those of Sinnott. Thus, the gradient of growth rates found by him does not hold since in all the tomato varieties the vascular tissue grows most rapidly. However, in the latter some secondary growth occurred, although the curve which shows the relation of growth of vascular cylinder to stem tissue remains a straight line, indicating no change in relative growth within the beginning of secondary growth. Aside from this, the difference between rate of growth in cortex and pith holds as in Sinnott's material, although the differences are not as extreme as those found by him.

Within the primary tissues cell number seems to be determined in the meristem. Cell size is directly related to the distance of those cells from the meristem. The fact that the cells in the cortex are much smaller than those in the pith may be related to the slower growth of that tissue. The persistence of cell division in the epidermis may be related to the smaller ultimate size of the cells which may be under functional control. It is generally assumed that pith and cortical cells play a comparatively small rôle in the physiology of the plant. The evidence found here for cell number in general points directly to the conclusion that cell number may be genetically controlled without any influence upon cell size.

Between the "pure" lines (varieties) the differences are largely meristematic in origin. Cell number certainly is, and likewise size of pith. The rate of growth of vascular tissue is different in the different types but there is a regularity in the difference. The smaller the stem the more rapid the growth of vascular tissue. The reason for this may be connected with the physiology of the plant. Although the leaves are smaller on the small-stemmed types, the length of the internodes is the same, with one exception, so that approximately the same number of leaves is produced. Thus transpiration in the thin-stemmed types would not be a great deal less than in the thick-stemmed types. Although the vascular cylinder grows more rapidly there is never actually as much in the small-stemmed as in the large-stemmed types for the number of leaves which it supports. Numerous instances of increase in vascular tissue in response to demand exist in the literature. Of course, in this present case the differences in growth rates of the vascular tissue may be the result of genetic factors, but it seems more plausible to consider it in the nature of a secondary and physiological response.

The reason for the decreasing rate of growth in the cortex is not obvious. Since the growth rate of the cortex is smallest where the growth rate of the vascular tissue is greatest there appears to be a compensatory effect. This suggests that perhaps the functional demand cited in the previous paragraph may determine the distribution of food or growth hormones and so account for these differences in growth rate. This seems to be in contradiction to Sinnott's hypothesis that differences in rate of growth of cortex and pith determine the position of the vascular cylinder. It is difficult to imagine a mechanism of control which would act first on the cortex and secondarily on the vascular tissue since their relative functional importance is reversed. However, if the control is directly genetic such action is possible.

SUMMARY

The development of the stem was studied in three varieties of *Lyco-persicum esculentum* and one variety of *L. pimpinellifolium*, in two hybrids between the species, and in one F_2 grown from one of the hybrids.

It was found that the rate of increase in diameter of stem with reference to the distance from the stem tip is the same in all types in spite of large initial and ultimate differences.

The length of internodes at corresponding distances from the meristem in plants of the same age is approximately the same in all types studied except in one variety of *L. esculentum*, Dwarf Champion, in which internode length is less. In general the internode below a branch is shorter than the one above. This branch effect is greatest in the thick-stemmed types.

The rate of growth of the different internal tissues is not the same. In general the pith increases in cross-sectional area at the same rate as the stem; the vascular cylinder enlarges faster and the cortex slower.

In the thinner-stemmed types the rate of growth of the vascular tissue as compared with growth of the stem is more rapid than in the thicker-stemmed types, and the rate of growth of the cortical tissue is correspondingly slower.

Cell cross-sectional area in the pith and in the cortex increases at the same rate as cross-sectional area of pith and cortex.

Epidermal cell number and cell size increase as the area of the stem increases.

Cell size in the cortex and in the pith in all but Dwarf Champion is the same at equal distances from the stem tip.

The differences in size of cortical and pith tissues in the different varieties is the result of differences in cell number. The hybrids lie intermediate between their parents and the positions of the F_2 plants indicate segregation and thus that cell number is inherited. No F_2 plant lies outside the cell number range of the parents.

The anatomical pattern possesses a regularity with relatively slight deviations which suggest a generic rather than a specific mechanism of control. Whereas minor deviations are under control of genetic factorial combinations that are characteristic of the several varieties and species, for *L. pimpinellifolium* has been held to be different specifically from *L. esculentum*, it is evident that for the genus *Lycopersicum* the mechanism involved is the same in all types.

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Additions to Florida Fungi—II [1]

WILLIAM A. MURRILL

Russula Arnoldae sp. nov.

Pileo convexo-depresso, 8–9 cm. lato, atropurpureo, sapore grato; sporis globosis, 6–8μ, stipite roseo, 7 $\times$ 1.5 cm.

Pileus convex to slightly depressed, solitary, 8–9 cm. broad; surface slightly viscid, pruinose to glabrous, smooth, atropurpureous, darker at the center; margin even, entire, not peeling readily; context thick, white, unchanging, odorless, mild; lamellae adnate, some forked at the base, equal, broad, medium distant, entire, pallid to flavous; spores globose to subglobose, spinulose, ochroleucous under microscope, 1–guttulate, 6–8μ; stipe subequal, smooth, glabrous, roseous, 7 $\times$ 1.5 cm.

Type collected by Lillian E. Arnold on the ground in a high hammock at Sugarfoot, near Gainesville, Fla., Sept. 25, 1938 (*F 18230*). A very handsome, highly-colored species with yellow, spinulose spores and mild flesh.

Russula floridana sp. nov.

Pileo convexo-depresso, 8 cm. lato, viscido, glabro, purpureorubro; sporis albis, ellipsoideis, 6–8 $\times$ 4–6μ, stipite albo, 8 $\times$ 2 cm.

Pileus convex to somewhat depressed, solitary, 8 cm. broad; surface viscid, smooth, glabrous, uniformly purple-red, cuticle not readily separable, margin entire, tuberculate-striate; context white, mild, odorless, yellowish when dry; lamellae adnate, mostly equal, medium distant, broad, entire, white, gray in dried specimens; spores white in mass, broadly ellipsoid, distinctly echinulate, 1–guttulate, 6–8 $\times$ 4–6μ; stipe equal, smooth, glabrous, white, slightly grayish or yellowish when dry, 8 $\times$ 2 cm.

Type collected by W. A. Murrill on the ground in woods at Gainesville, Fla., June 30, 1938 (*F 18084*). A handsome species of rare occurrence.

Russula heterospora cremea var. nov.

Pileo cremeo, lamellis sinuatis, sporis ellipsoideis, glabris, 10 $\times$ 6μ, stipite albo, 4 $\times$ 1–1.7 cm.

Pileus convex to depressed, solitary, 7 cm. broad; surface slightly viscid, smooth, glabrous, cremeous with a few rusty spots, peeling very readily, margin even; context thin, white, mild; lamellae distinctly sinuate, broad, subdistant,

some forked at the middle, white; spores cremeous in mass, ellipsoid, smooth, hyaline, about 10 $\times$ 6μ; stipe tapering downward, smooth, white, glabrous, 4 $\times$ 1–1.7 cm.

Type collected by West, Arnold and Murrill on the ground in a high hammock at Sugarfoot, near Gainesville, Fla., Sept. 29, 1938 (*F 18343*). Very different in appearance from the typical form of *R. heterospora* Beardslee so common about Gainesville, which is rosy-purple-olivaceous on the surface and has more slender spores.

Russula tuberculata sp. nov.

Pileo convexo-depresso, 6 cm. lato, praestriato, albo et rubro; lamellis angustatis, sporis globosis, tuberculatis, 8–11μ; stipite roseo-albo, 4 $\times$ 1.5–2 cm.

Pileus convex to depressed, solitary, 6 cm. broad; surface somewhat viscid, glabrous, conspicuously striate, not peeling readily, white with reddish patches or spots over the center; context thin, white, mild, odorless; lamellae adnate, equal, many forked at the base, medium distant, narrow, white, entire; spores perfectly globose, coarsely tuberculate, white in mass, 8–11μ; stipe flattened, tapering downward, smooth, glabrous, white tinged with rose, 4 $\times$ 1.5–2 cm.

Type collected by West, Arnold and Murrill on the ground in a high hammock at Sugarfoot, near Gainesville, Fla., Sept. 29, 1938 (*F 18344*). Very striate with narrow gills and globose spores covered with large papillate warts.

Lactaria parvula sp. nov.

Pileo convexo-depresso, 2 cm. lato, pallido, zonato, sapore grato, lacte albo; sporis subglobosis, 4–5μ, stipite albo, 3 $\times$ 0.6 cm.

Pileus convex to slightly depressed, solitary, 2 cm. broad; surface slightly viscid when moist, smooth, glabrous, zonate, whitish with a rosy-isabelline tint, margin entire, even; context white, unchanging, mild; lamellae tapering behind, arcuate, narrow, crowded, forked, entire, white, unchanging; latex white, unchanging; spores globose or subglobose, finely tuberculate, hyaline, 4–5μ; sterile cells abundant, conic, pointed, hyaline, projecting about 15 $\times$ 8μ; stipe equal, smooth, glabrous, white, unchanging, 3 $\times$ 0.6 cm.

Type collected by E. West and W. A. Murrill on the ground in Sanchez Hammock, eleven miles northwest of Gainesville, Fla., July 23, 1938 (*F 18214*). A small, whitish species with small spores and large, conic sterile cells on the edges of the gills.

Lactaria Westii sp. nov.

Pileo convexo-depresso, 5–7 cm. lato, pallido, piperato; sporis globosis, valde tuberculatis, 9μ; stipite albo, pruinoso, 2–4 × 0.8–1.3 cm.

Pileus convex to slightly depressed, solitary to gregarious or subcespitose, 5–7 cm. broad; surface soft, dry, minutely pruinose to glabrous, smooth, varying from white to pale avellaneous-isabelline, pallid or partly isabelline when dry, margin even, entire, glabrous; context white, unchanging, odorless, acrid; lamellae attenuate behind, slightly decurrent, narrow, close to medium distant, inserted, entire, yellowish to dirty-brownish-yellow; latex white, unchanging; spores perfectly globose, strongly tuberculate, hyaline, about 9μ; stipe usually short, equal or tapering downward, smooth, pruinose, especially above, white, unchanging, 2–4 × 0.8–1.3 cm.

Type collected by E. West and W. A. Murrill under an oak at Newnan's Lake, Fla., July 30, 1938 (*F 18218*). Also collected by West and Murrill under oaks at Kanapaha Sink, July 26, 1938 (*F 18085*), and at Arredonda, July 29, 1938 (*F 18086*). Suggesting *L. praeseriflua* Murrill when first seen but finely pruinose to glabrous and having acrid milk.

Entoloma Grayanum caespitosum var. nov.

Pileo convexo, caespitoso, sporis 10 × 8μ; stipite albo, 4–5 × 0.5–1 cm.

Pileus broadly convex, densely cespitose, 4–5 cm. broad; surface smooth, glabrous, opaque, avellaneous-umbrinous, margin incurved, even, entire to undulate; context white, taste and odor strongly farinaceous; lamellae adnate, pallid to pale-pink; spores decidedly angular, apiculate, 1-guttulate, pink, about 10 × 8μ; stipe smooth, white, glabrous, tapering upward, 4–5 × 0.5–1 cm.

Type collected by W. A. Murrill on the ground in woods at Gainesville, Fla., July 1, 1938 (*F 18248*). Densely clustered and having a shorter stipe than the typical form.

Entoloma pinicola sp. nov.

Pileo convexo-subexpanso, 2.5–3.5 cm. lato, albido, disco isabellino; sporis angulatis, 9–11 × 6–7μ, stipite albo, 5 × 0.3–0.5 cm.

Pileus convex to subexpanded, gregarious, 2.5–3.5 cm. broad; surface smooth, glabrous, satiny, whitish, isabelline on the conic umbo, margin even, entire; context very thin, odorless, mild to slightly astringent, white; lamellae sinuate with decurrent tooth, ventricose, inserted, broad behind, medium distant, the edges uneven and more or less toothed; spores decidedly angular, usually 5-sided or kite-shaped, apiculate, 1–2-guttulate, pale-pink, 9–11 × 6–7μ;

cystidia none; stipe tapering upward, smooth, glabrous, shining, white, about 5 × 0.3–0.5 cm.

Type collected by West, Arnold and Murrill on the remains of a much-decayed pine log in Prairie Creek Hammock, near Gainesville, Fla., July 15, 1938 (*F 18252*). Unusual in its color, substratum, and slender stem. Herbarium specimens are umbrinous throughout and show white streaks of some compound of calcium on the surface of the cap.

Entoloma subcommune sp. nov.

Pileo convexo-subdepresso, umbonato, 2.5–3 cm. lato, avellaneo-umbrino, odore et sapore farinaceo; sporis angulatis, 8–10 × 6–7μ, stipite avellaneo, 4 × 0.3 cm.

Pileus convex to slightly depressed with a small flat umbo, gregarious to cespitose, 2.5–3 cm. broad; surface smooth, glabrous, avellaneous-umbrinous, blackish when dry; margin even, entire or slightly lobed; context thin, white, with strong farinaceous odor and taste; lamellae sinuate, broad behind, fragile, white to pink, inserted, medium distant, edges thin, undulate to eroded; spores decidedly angular, apiculate, 1–2–guttulate, pink, broadly ellipsoid in outline, 8–10 × 6–7μ; cystidia none; stipe equal, smooth, glabrous, avellaneous, whitish-mycelioid at the base, about 4 × 0.3 cm.

Type collected by West and Murrill on the ground in Kelley's Hammock, ten miles northwest of Gainesville, Fla., Aug. 3, 1938 (*F 18241*). Also collected by Murrill, Weber and West near Gainesville, Dec. 14, 1926 (*F 10020*). Near *E. commune* Murrill but with different spores.

Nolanea alachuana sp. nov.

Pileo convexo-umbilicato, 1–2.5 cm. lato, striato, avellaneo; sporis angulatis, 7–9μ, stipite avellaneo, 3–5 × 0.1–0.3 cm.

Pileus conic to broadly convex, not fully expanding, usually umbilicate, gregarious or scattered, 1–2.5 cm. broad; surface avellaneous, glabrous, shining, striate-sulcate to the disk, margin entire; context thin, pallid, odorless, mild; lamellae sinuate, broad, triangular, medium distant, inserted, entire, pallid to dull-pink, at length dark-isabelline; spores globose in outline, moderately angular, strongly apiculate, 1–guttulate, 7–9μ; cystidia none; stipe equal, smooth, glabrous, shining, concolorous, whitish-mycelioid at the base, 3–5 × 0.1–0.3 cm.

Type collected by West and Murrill on the ground in Kelley's Hammock, ten miles northwest of Gainesville, Fla., July 19, 1938 (*F 18246*). Also at the same place, July 19, 1938 (*F 18243*), and Aug. 3, 1938

(*F 18242*). The spores distinguish it at once from species of similar appearance. They remind one of grains of corn.

Cortinarius Arnoldae sp. nov.

Pileo convexo, praeviscido, badio, 4 cm. lato; lamellis lilacinis, sporis tuberculatis, 15–17 × 6–7μ; stipite ventricoso, lilacino, 9 × 1–1.5 cm., annulo fibroso, albo.

Hymenophore covered with a thick, slimy universal veil resembling the white of an egg; pileus campanulate, not fully expanded, slightly umbilicate, solitary, 4 cm. broad; surface smooth, glabrous, uniformly badious, margin even, entire, incurved, lilac; context thin, pallid, mawkish, odorless; lamellae adnate, arcuate, subdistant, inserted, entire, pale-lilac, becoming fulvous; spores pip-shaped from above, turtle-shaped from the side, coarsely tuberculate, deep-ferruginous, 15–17 × 6–7μ; stipe oblong-fusiform, smooth, glabrous, lilac, dirty-cremeous at the base, 9 × 1–1.5 cm.; annulus ample, white, · cobwebby, attached 1 cm. from the apex of the stipe.

Type collected by Lillian E. Arnold on the ground in a high hammock at Sugarfoot, near Gainesville, Fla., Sept. 29, 1938 (*F 18352*). A beautiful species, very rare, with spores shaped like a young box-turtle and covered with warts like a hop-toad. I have never seen a more glutinous agaric. *C. splendidus* Peck is a near relative.

Ceriomyces rubricitrinus sp. nov.

Pileo convexo, 5–8 cm. lato, glabro, testaceo ad latericio; tubulis citrinis, sporis fusoideis, 15 × 5μ; stipite reticulato, rubropunctato, 5 × 1.5–1.8 cm.

Pileus broadly convex, gregarious, 5–8 cm. broad; surface smooth, glabrous, testaceous to latericious, margin even, entire; context white with a yellowish tint, quickly turning blue when wounded, taste subacid; tubes slightly depressed at the stipe, slender, citrinous, becoming blue when wounded, mouths small, not stuffed; spores oblong-fusiform, smooth, yellowish-brown, 15 × 5μ; stipe tapering upward, 5 × 1.5–1.8 cm., yellow above, reddish-dotted below, reticulate, roseous within when cut except at the base, where it becomes bluish.

Type collected by W. A. Murrill on a lawn near a laurel oak in Gainesville, Fla., July 2, 1938 (*F 17321*). I first tried to make this a red variety of *C. subsensibilis* Murrill but the differences were too great. Only the one collection was made.

Gyroporus deflexus sp. nov.

Pileo convexo, 4.5 cm. lato, atro-griseo, subtomentoso, sapore grato; tubulis albis, parvis, sporis ochroleucis, 10–12 × 3μ; stipite glabro, 5 × 1 cm.

Pileus convex, gregarious, 4.5 cm. broad; surface dry, smooth, subtomentose, dark-avellaneous to umbrinous, margin entire, sterile, deflexed; context thick, white, unchanging, sweet; tubes plane, small, white, becoming yellowish where bruised; spores oblong-fusiform, smooth, ochroleucous, 10–12 × 3μ; stipe equal, glabrous, white above, avellaneous below, marked with parallel ridges, 5 × 1 cm.

Type collected by West, Arnold and Murrill on the ground in rather dry oak-pine woods at Magnesia Springs, Fla., July 15, 1938 (*F 18216*). Similar to *Ceriomyces subtomentosus* (L.) Murrill in shape but dark-gray in color with small, white tubes and strongly deflexed margin.

Gyroporus Rhoadsiae sp. nov.

Pileo convexo-subexpanso, 6–8 cm. lato, albido, felleo; sporis fusoideis, hyalinis, 12 × 4μ; stipite albo, reticulato, 6–8 × 1.5–2 cm.

Pileus convex to subexpanded, thick, gregarious, 6–8 cm. broad; surface dry, smooth, glabrous, whitish, shining when dried; margin thin, even, entire, projecting; context moderately thick, white, unchanging, very bitter; tubes angular, 5–10 mm. long, 1–2 to a mm., thin-walled, white, unchanging; spores oblong-fusiform, smooth, hyaline, about 12 × 4μ; stipe equal or nearly so, glabrous, beautifully reticulate above, white, unchanging, 6–8 × 1.5–2 cm.

Type collected by Louise and Arthur S. Rhoads on the ground under slash pine and shrubs at the margin of Lake Rosa, two miles east of Melrose, Fla., Sept. 8, 1938 (*F 18199*). A large, whitish, bitter species, becoming shining and almost pure-white when dried.

Gyroporus stramineus sp. nov.

Pileo convexo-subexpanso, 6 cm. lato, stramineo, sapore grato; sporis ochroleucis, 9–14 × 3μ, stipite albo, 4 × 1 cm.

Pileus convex subexpanded, solitary, 6 cm. broad; surface dry, smooth, glabrous, stramineous, whitish and shining when dried; margin even, undulate, fertile; context white, mild; tubes somewhat decurrent, 5 mm. long, 2–3 to a mm., isabelline at maturity, fulvous when dried; spores sausage-shaped, smooth, ochroleucous, 9–14 × 3μ; stipe equal, smooth, glabrous, white, unchanging, about 4 × 1 cm.

Type collected by W. A. Murrill in turkey-oak woods at Gainesville, Fla., Sept. 10, 1938 (*F 18156*). There are no rosy tints as in *B. roseialbus* Murrill; the flesh is mild; and the stem not at all reticulate.

Boletus pseudogranulatus sp. nov.

Pileo convexo-plano, 6 cm. lato, viscido, roseo-isabellino, subfelleo; tubulis ochroleucis, non punctatis, sporis fusoideis, 8–10 × 2.5–3μ; stipite sulphureo, reticulato, 4 × 1.5–2 cm.

Pileus convex to plane, gregarious, about 6 cm. broad; surface decidedly viscid, dark rosy-isabelline, margin even, projecting, appendiculate; context white, unchanging, slightly bitter and mawkish, reaching 1 cm. thick; tubes adnate or decurrent, reaching 5 mm. long, 2–4 to a mm., not stuffed, ochroleucous, not changing when cut; edges entire, without resinous dots; spores oblong-fusiform, smooth, granular, hyaline under the microscope, 8–10 × 2.5–3μ; stipe enlarged below, solid, reticulate nearly to the base, sulphuryellow without and within, without resinous dots, 4 × 1.5–2 cm.; veil so reduced that only a few fibers are left on the stipe.

Type collected by W. A. Murrill on the ground under a pine in Gainesville, Fla., Oct. 2, 1938 (*F 18342*). It was surprising to find specimens so similar to *R. granulatus* (L.) P. Karst. without resinous dots on either tubes or stem and having the latter beautifully reticulated. In drying the context first changes to yellow and at length to rosy-isabelline, while the tubes become melleous.

Since this species has no true annulus it does not rightfully belong in the genus *Boletus* as limited by me, but there is no other place to put it. In *Rostkovites* glandular dots are essential and my conscience will not allow me to assign it to *Gyroporus*, so far removed from its obvious relatives. In *Boletus* there are species like *B. Clintonianus* Peck without glandular dots and with slight reticulations on the stipe; so let us consider our present problem child as having a very much reduced veil, which leaves only fragments on the margin and a ring-trace on the stipe.

Tyromyces leucomallellus sp. nov.

Pileo effuso-reflexo, 0.5–2 cm. lato, albo; tubulis 1–2 mm. longis, angulatis, albis; sporis 4–5 × 1μ.

Effused-reflexed, mostly resupinate, subcircular to elliptic, 0.5–2 cm. broad, the reflexed portion an elevated margin or a narrow strip a few millimeters wide; surface soft, pubescent, azonate, white, becoming slightly ferruginous when bruised; margin thin, even, undulate; context thin, fibrous, white, unchanging; tubes 1–2 mm. long, 3–4 to a mm., angular, thin-walled, entire, white, brownish where bruised, collapsing and somewhat lacerate-dentate with age; spores copious, allantoid, smooth, hyaline, 2–3–guttulate, about 4–5 × 1μ.

Type collected by W. A. Murrill on a dead log of *Taxodium distichum* at Newnan's Lake, Fla., April 24, 1938 (*F 18231*). Cotype the same time,

place and host (*F 18239*). An inconspicuous white species somewhat resembling *T. leucomallus* (Berk. & Curt.) Murrill and in some ways suggesting *Spongipellis fragilis* (Fr.) Murrill, but much smaller than either and almost wholly resupinate. The guttae in the spore are very large, appearing like a row of beads.

Tyromyces magnisporus sp. nov.

Pileo turbinato, 4–5 × 2–3 cm., subtomentoso, albo vel cremeo, praefelleo; tubulis albis, angulatis, sporis ovoideis, 10–12 × 5–7μ.

Pileus irregularly turbinate, usually clasping, subimbricate, solitary, 4–5 cm. broad and 2–3 cm. thick behind; surface plane or uneven, finely tomentose, white or cremeous, margin even, very irregular, undulate or lobed, fertile; context very bitter, fragant like anise, spongy-fleshy, fragile when dry, white, unchanging; tubes about 5 mm. long, 2–3 to a mm., rather thin-walled, angular, entire, white, usually becoming isabelline on drying; spores elongate-ovoid or subellipsoid tapering at one end, smooth, hyaline, often 1–guttulate, copious, 10–12 × 5–7μ.

Type collected by West and Murrill on a small dead hardwood stub in Kelley's Hammock, ten miles northwest of Gainesville, Fla., July 19, 1938 (*F 17916*). Also collected by West and Murrill on a dead hardwood stub in Sanchez Hammock, July 23, 1938 (*F 18238*), and on a dead hardwood stub in Kelley's Hammock, Aug. 3, 1938 (*F 17395*). Conspicuous by reason of its encircling habit, large spores, and bitter taste.

Tyromyces Newellianus sp. nov.

Pileo effuso-reflexo, imbricato, azonato, ochraceo, rugoso; tubulis, albis, parvis, sporis 3–4 × 1μ.

Pileus effused-reflexed, imbricate, the reflexed portion sessile, dimidiate to laterally elongate, 1–1.5 × 1–4 × 0.2–0.4 cm.; surface azonate, rough, scabrous to rugose or subvirgate, ochraceous, isabelline when dried; margin thin, even, glabrous, entire to undulate; context thin, white, unchanging, friable; tubes slender, angular, thin-walled, 3–4 to a mm., white and unchanging within, edges entire to dentate, white, becoming ferruginous when bruised and somewhat collapsed on drying; spores allantoid, smooth, hyaline, copious, about 3–4 × 1μ; cystidia none.

Type collected by W. A. Murrill on a rotten hardwood log in a hammock at Gainesville, Fla., Sept. 23, 1938 (*F 18215*). Having the type of spore found in *T. caesius* (Schrad.) Murrill but with color and surface entirely different. Dedicated to Dr. Wilmon Newell, for many years Director of the Florida Agricultural Experiment Station.

Tyromyces pini-glabrae sp. nov.

Pileo semi-resupinato, 1.5–3 cm. lato, tomentosulo, albo; tubulis merulioideis, albis, sporis globosis, 3–4μ.

Pileus semi-resupinate, 1.5–3 cm. broad, the reflexed portion dimidiate to elongate, thin, flexible, becoming very rigid on drying, 0.5–1 × 1–3 × 0.1–0.2 cm.; surface uneven, slightly tomentose, milk-white, unchanging; margin even, undulate to lobed, slightly opaque-brownish where bruised, decurved on drying; context homogeneous, hygrophanous, whitish, appearing horny and brownish when dry; hymenium merulioid when young, mature tubes shallow, irregular, angular, thin-walled, 2–4 to a mm., white, unchanging, entire; spores few, globose, smooth, hyaline, 3–4μ.

Type collected by West, Arnold and Murrill on a dead log of *Pinus glabra* Walt. in Beech Woods, near Santa Fé, Fla., July 13, 1938 (*F 18235*). A milk-white species with very shallow pores found once in the only beech grove known in Alachua County.

Tyromyces pseudolacteus sp. nov.

Pileo dimidiato, 2–3 cm. lato, hirsuto, albo; tubulis parvis, albis, brevibus sporis ovoideis, 3 × 2μ.

Pileus sessile, imbricate, dimidiate to reniform, convex, 1–2 × 2–3 × 0.5–1 cm.; surface sodden, azonate, rough, hirsute or hirsute-tomentose, white, unchanging; margin acute, even, entire to undulate, white, becoming brown when dried; context homogeneous, soft, fibrous, white, unchanging, drying soft-corky and subfragile, reaching 1 cm. thick; tubes delicate, short, angular, thin-walled, 5–6 to a mm., white, unchanging, entire to dentate; spores ovoid, smooth, hyaline, 1–guttulate, about 3 × 2μ; cystidia none.

Type collected by West and Murrill on a fallen dead oak stick in woods at Gainesville, Fla., June 3, 1938 (*F 17396*). Suggesting the true *Polyporus lacteus* of Fries as it occurs in Sweden but without the allantoid spores of that species. An older specimen measuring 4 × 5 × 2 cm., which seems to belong here, has the same hirsute surface and similar spores but the slender tubes have partially collapsed and the edges are lacerate. It was collected by West and Murrill on an oak log in Gainesville, Oct. 24, 1932 (*F 18253*).

Poria cubitispora sp. nov.

Prae-effuso, adnato; tubulis albis, 3–4 mm. longis, parvis, angulatis, praefelleis, fragilibus; sporis allantoideis, hyalinis, 2.5–3 × 1μ; cystidiis 30 × 10μ.

Widely effused, continuous for many centimeters, inseparable, about 5 mm. thick; margin slight, appressed, white, soon inconspicuous; context very thin,

white; hymenium even, glistening, white with a few luteous stains, dark-isabelline where bruised, cremeous when dried; tubes 3–5 mm. long, about 5 to a mm., soft, juicy, fragile, intensely bitter, mouths fairly regular, angular, edges thin, entire; spores short, sharply curved, smooth, hyaline, very abundant, $2.5 \times 1\mu$; cystidia abundant, tapering from a thick base, pointed or obtuse, encrusted, projecting about $30 \times 10\mu$.

Type collected by West, Arnold and Murrill on the side of a much-decayed log of *Nyssa sylvatica* Marsh. in a high hammock at Sugarfoot, near Gainesville, Fla., Sept. 29, 1938 (*F 18341*). A striking species as bitter as quinine, with spores that remind one of boiled shrimp. In *P. griseoalba* (Peck) Sacc. and *P. sulphurella* (Peck) Sacc. the spores measure about $4 \times 1\mu$ and vary from cylindric to slightly allantoid. In this species they are short and curved almost as much as an elbow joint. Under the microscope they seem to wriggle about like half-coiled insect larvae. Mr. West assisted me with the microscopic examination.

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made:

Ceriomyces rubricitrinus = **Boletus rubricitrinus**
Gyroporus deflexus = **Boletus deflexus**
Gyroporus Rhoadsiae = **Boletus Rhoadsiae**
Gyroporus stramineus = **Boletus stramineus**
Tyromyces leucomallellus = **Polyporus leucomallellus**
Tyromyces magnisporus = **Polyporus magnisporus**
Tyromyces Newellianus = **Polyporus Newellianus**
Tyromyces pini-glabrae = **Polyporus pini-glabrae**
Tyromyces pseudolacteus = **Polyporus pseudolacteus**

HERBARIUM FLORIDA AGRICULTURAL EXPERIMENT STATION
  GAINESVILLE, FLORIDA

Descriptions of Tropical Rusts—II [1]

GEORGE B. CUMMINS

(WITH TEN FIGURES)

Puccinia amphiospora (Jacks. and Holw.) comb. nov. (fig. 1). (*Uredo amphiospora* Jacks. and Holw.; Jackson in Mycologia **24**: 72. 1932.)

Telia not seen; teliospores in the uredia ellipsoid or oblong-ellipsoid, rounded above, usually narrowed below, moderately constricted at the septum, 16–20 × 29–38μ; wall light cinnamon-brown, smooth, 1μ thick, the pore in the upper cell apical and covered by a small, hyaline umbo which disappears at germination, pore in lower cell at septum; pedicel hyaline, fragile, about one-half the length of the spore but usually broken near the spore. The spores germinate at once.

Jackson (*l.c.*) reported three collections on *Hyptis spicata* Poit. from Bolivia, two of which were issued in Reliq. Holw. as numbers 415 and 420. Both of them have teliospores. The type was collected by the Holways at Cochabamba, Bolivia, Feb. 25, 1920 as number 324 (Reliq. Holw. 415).

The occurrence of two kinds of urediospores, one of which is considered to be amphisporic, is the characteristic feature of the species.

Puccinia unilateralis (Arth.) comb. nov. (fig. 8). (*Uredo unilateralis* Arth., Bull. Torrey Club **45**: 155. 1918.)

Pycnia epiphyllous, 2 or 3 in a group, subepidermal, globoid, 130–200μ diam. Aecia hypophyllous opposite the pycnia, few in a group on spots up to 3 mm. diam., subepidermal, caeomoid, blister-like, orange, usually elongate, 0.1–0.3 × 0.5–1 m. or larger and irregular by confluence, peridium none; aeciospores catenulate, oblong, broadly ellipsoid or globoid, 20–28 × 26–35μ; wall 2μ thick, hyaline, closely and rather coarsely verrucose with squarish or irregular, flat tubercles. Uredia hypophyllous, scattered or in more or less circinate groups, 0.2–0.8 mm. diam., pulverulent, dark cinnamon-brown; urediospores asymmetrical, obovoid with the pore face-view, reniform with the pore lateral, 20–26 × 26–32μ; wall cinnamon-brown, 1.5μ thick, echinulate except around the single pore located somewhat below the equator in the concave surface. Telia hypophyllous, subepidermal, pulvinate, yellowish, waxy in appearance but becoming cinereous from germination; teliospores sessile on a cellular hymenium, oblong or clavate, rounded above, narrowed below, constricted at the septum, 18–27 × 45–70μ; wall hyaline, 1–1.5μ thick at sides,

6–12μ at apex, less so or similarly thickened below the septum; the pore apical in upper cell, next the septum in lower cell. The teliospores germinate at once.

The description of pycnia and aecia was drawn from a specimen collected by J. H. Faull, Mt. San Felipe, Oaxaca, Mexico, Dec. 5, 1938 on *Geranium* sp. Kern and Whetzel (Journ. Dept. Agric. Porto Rico 14: 347.
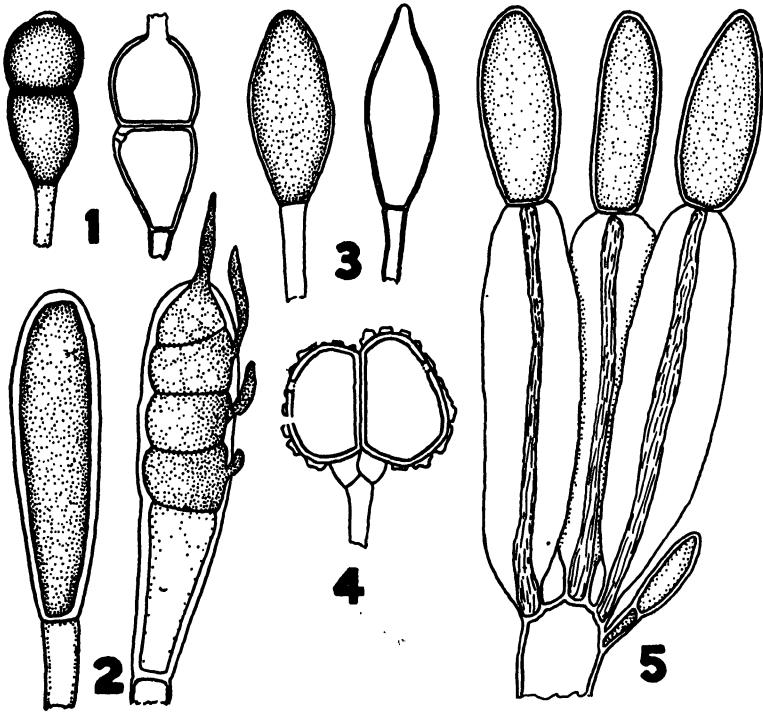
Fig. 1. Teliospores of *Puccinia amphiospora.* ×650.
Fig. 2. Teliospores of *Acrotelium lucumae.* ×650.
Fig. 3. Teliospores of *Scopella cryptostegiae.* ×650.
Fig. 4. One teliospore of *Dicheirinia solenioides.* ×650.
Fig. 5. Teliospores of *Scopella bauhiniicola.* ×650.

1930) have previously described pycnia and aecia of what probably should be considered the same species on *G. hirtum* Willd. from Colombia (*Chardon 596*).

Telia are present in Faull's specimen but are described from the type of *Uredo unilateralis* on *G. mexicanum* (issued in Barth. N. Am. Ured. *2481*) where they were found to be numerous. Telia are also present on Chardon's specimen, which Dr. F. D. Kern kindly sent me. The teliospores differ noticeably from North American specimens in being narrower (14–18 × 58–73μ) and in having a thinner apical wall (2–4μ). No differ-

ences were evident in the aecia and uredia. The species is known to occur also in Ecuador on *G. chilloense* Willd. and *G. sodiroanum* Kunth but the collections have only uredia.

The attachment of the teliospores is difficult to observe in either crushed mounts or sections. No pedicels have been seen. The spores appear rather to be sessile upon a basal cellular hymenium with two or three attached to the unit cells which are neither elongate nor laterally free.

Puccinia poikilospora sp. nov. (fig. 10).

Pycnia et aecia ignota. Uredia hypophylla, subepidermalia, pustulata, sparsa vel aggregata, cinnamoneo-brunnea; urediosporae obovoideae, ellipsoideae vel late ellipsoideae, 18–23 $\times$ 25–33μ; membrana pallide cinnamomeo-vel aureo-brunnea, 2–3μ cr., moderate echinulata, poris germ. 3 vel 4 aequatorialibus. Telia hypophylla, subepidermalia, pustulata, sparsa vel circinata, brunneo-atra; teliosporae variabiles, ex cellulis 2–4 compositis, oblongae vel clavatae, 16–23 $\times$ 33–50μ; membrana 1.5–2μ cr., 4–9μ supra, castaneo-brunnea; pedicellis aureo-brunneis, 20–45μ longis.

On *Smilax spinosa* Mill., Jutiapa, Guatemala, Dec. 21, 1938, *J. R. Johnston 1425*. Type specimen in the Arthur Herbarium, Purdue University Agricultural Experiment Station.

This interesting rust has much the gross appearance of *Puccinia smilacis* Schw. but the sori are larger, more blister-like and the epidermis usually opens by a slit. The telia have a tendency to occur in a circle about the uredia and, like the uredia, remain partially covered by the epidermis. Variation in the septation of the teliospores is conspicuous, with two-, three- and four-celled spores occurring in approximately equal proportions. Mesospores are rare. The cells may all be arranged longitudinally or the upper two may be horizontally arranged upon the subjacent cell. Still greater irregularity in conformation occasionally occurs.

Bubakia erythroxylonis (Graz.) comb. nov. (*Uredo erythroxylonis* Graz., Bull. Soc. Myc. Fr. 7: 152. 1891.)

Telia hypophyllous, circinate about the uredia, subepidermal, blackish brown, 85–100μ in diameter or becoming confluent; teliospores in crusts 2–4 spores thick, individual spores irregularly arranged, not catenulate, oblong or cuboid, 7–12 $\times$ 12–26μ, the lower ones usually irregular; wall chestnut-brown, smooth, 1μ thick at sides, 1.5–2.5μ apically in the outer spores, not strongly adherent laterally, sessile.

This description of telia is based upon a collection on *Erythroxylon havanense* Jacq., Vivijagua, Isle of Pines, Cuba, Feb. 28–29, 1916, *N. L. Britton, E. G. Britton* and *Percy Wilson 15023*.

The telia are developed by the branching and septation of a few hyphae and usually originate beneath stomata. Prior to the formation of spores the hyphae become thick-walled and produce a cellular complex. The unit cells of this complex enlarge, become pigmented and ultimately become spores. The uppermost layer of spores is regularly arranged beneath the epidermis but the lower ones lack this regularity and vary more in shape. This irregularity within the sorus becomes more noticeable the larger the sorus becomes.

Dicheirinia solenioides (P. Henn.) comb. nov. (fig. 4). (*Uredo solenioides* P. Henn., Hedwigia **35**: 250. 1886.)

Telia not seen; teliospores in the uredia 2–celled, broadly ellipsoid, broader than high, vertically septate, constricted at the septum, 30–38μ broad by 23–26μ high; wall 1.5μ thick, chestnut-brown or darker, coarsely tuberculate with cubical or irregular warts 2–3μ high, pores one in each cell above the equator in the outer wall; pedicel short and fragile, hyaline, thin-walled, simple basally but horizontally 2–celled next the spore.

Hennings (*l.c.*) in his original description mentions having seen one teliospore and the Sydows (Monogr. Ured. **4**: 490. 1924) report that they also observed teliospores but were not convinced that they belonged with the uredia. There is no doubt that they do, however, because I have seen them attached in sections of the uredia.

This characteristic and appropriately named species is similar in appearance to *D. ormosiae* (Arth.) Cumm. The sori are abundantly provided with peripheral paraphyses which extend well above the surface of the host, curve inward and produce a sorus "solenioid" in appearance. *D. ormosiae* also has such a sorus but with the paraphyses much branched and botryoid rather than simple. Both species have a single pore in the urediospore, located next the hilum.

These studies are based upon three specimens, all collected by Ule at St. Catharina, Sao Francisco, Brazil on *Nectandra rigida* Nees. One bears Ule's number 90 but is without date, the second was issued in Rabenh. Fungi eur. *4243* and the third was collected April, 1885 but is without a number. Perhaps all represent a single collection.

Acrotelium lucumae (Arth. and Johnst.) comb. nov. (figs. 2, 7). (*Uredo lucumae* Arth. and Johnst., Mem. Torrey Club **17**: 169. 1918.) (*Uraecium lucumae* Arth., Bull. Torrey Club **60**: 467. 1933.)

Telia hypophyllous, developing in the uredia or separately, subepidermal, round, oval or irregular in outline, 0.1–1.0 mm. in diameter, waxy, yellowish;

teliospores 1-celled, borne in groups on light brownish or hyaline, laterally free basal cells, pedicellate, cylindrical, rounded above, obtuse below, contents yellowish, 15–20 $\times$ 59–98μ in mature condition; wall hyaline, apparently slightly hygroscopic, smooth, 2.5–3μ thick; pedicel hyaline, thin-walled, about one-half as long as the spore and nearly as broad. The teliospores germinate at once by the formation of a 4-celled internal basidium in the upper one-half of the spore.
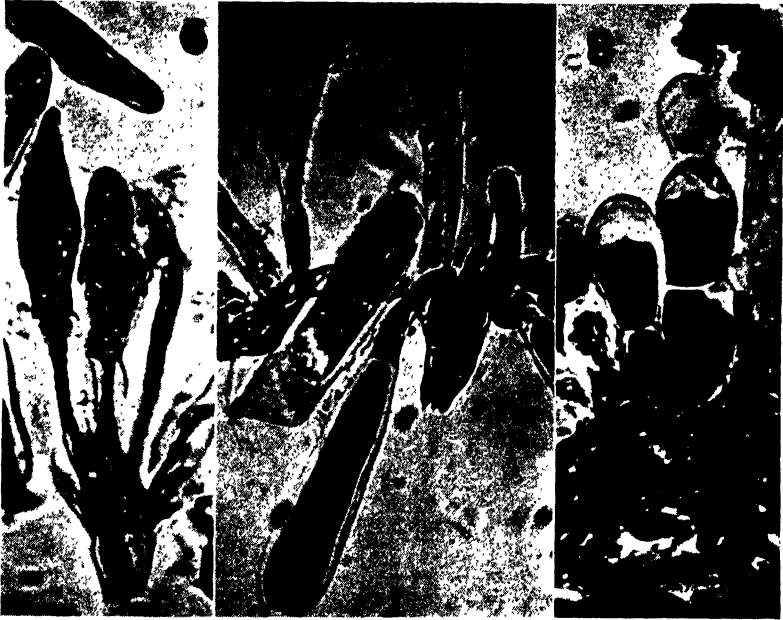
Fig. 6. *Scopella bauhiniicola;* photograph of a basal cell and attached teliospores (stained). $\times$ 625.

Fig. 7. *Acrotelium lucumae;* photograph of a basal cell and attached teliospores (stained). $\times$ 500.

Fig. 8. *Puccinia unilateralis;* photograph of a free-hand section of a telium, showing two teliospores (stained). $\times$ 650.

The description is drawn from a specimen received from Dr. Erdman West of the Florida Agricultural Experiment Station, collected by Geo. Ruehle at Homestead, Dade Co., Florida, Feb. 7, 1939. Telia are also present on the following specimens in the Arthur Herbarium: Santiago de las Vegas, Cuba, Feb. 23, 1916 and Mar. 5, 1916, J. R. Johnston *490* and *494*. All are on *Lucuma nervosa* A.DC.

The only previously described species of this genus is *Acrotelium ichnocarpi* Syd., in the Philippine Islands. Both *A. ichnocarpi* and *A. lucumae* have cylindrical, thick-walled teliospores but the basal cells

are much more conspicuous and larger in *A. lucumae*. Basal cells are not readily observable in *A. ichnocarpi*.

In *A. lucumae* the pycnia are subcuticular and the aecia uredinoid and similar to the uredia which follow. Only uredia and telia have been reported for *A. ichnocarpi*. There is, therefore, no very broad basis upon which to judge the relationship of the two species.

Scopella cryptostegiae (Vestergr.) comb. nov. (fig. 3). (*Uredo cryptostegiae* Vestergr., Svensk. Bot. Tidskr. **8**: 90. 1914).

Telia following in the uredia or separate, subepidermal, waxy in appearance, yellowish, pulvinate, small 0.1–0.2 mm. in diameter; teliospores produced in groups on straight or apically curved, laterally free basal cells, ellipsoid or ovoid, contents yellowish, 12–17 $\times$ 27–38μ; wall hyaline, smooth, uniformly 0.5–1.0μ thick, without a germ pore; pedicel shorter than or equal to the length of the spore, hyaline, thin-walled. The teliospores germinate at once by the apical elongation of the spore.

This description is drawn from the type collection on *Cryptostegia madagascariensis* Boj., collected by B. Palm at Majunga, Madagascar, April, 1912 and issued in Vestergr. Microm. rar. sel. *1660*.

The Sydows (Monogr. Ured. **4**: 431. 1924) considered that the species belonged in the genus *Hemileia* because of the shape and structure of the urediospores. They did not observe teliospores. *Hemileia* is excluded from consideration, however, because the sori do not emerge from the stomata as fascicles of hyphae. The hyaline basal cells are readily observable and each bears ten or more spores, usually apically and along one side. Frequently the basal cells are curved, with the spores produced along the upper convex side.

Scopella bauhiniicola (P. Henn.) comb. nov. (figs. 5, 6). (*Uredo bauhiniicola* P. Henn., Hedwigia **34**: 98. 1895.)

Telia hypophyllous in the old uredial infections, waxy, yellowish, pulvinate, 0.1–0.3 mm. in diameter or becoming confluent, subepidermal; teliospores borne in groups of 5–7 or more on short, clavate, laterally free basal cells, ellipsoid, ovoid or oblong-ellipsoid, 13–18 $\times$ 30–45μ, contents yellowish; wall hyaline, smooth, uniformly 1–1.5μ thick, without a germ pore; pedicels once and one-half to twice as long as the spore, with a central persistent strand and an outer hygroscopic portion which swells to broader than the spore and may ultimately dissolve, hyaline. The teliospores germinate at once by the elongation of the apex of the spore.
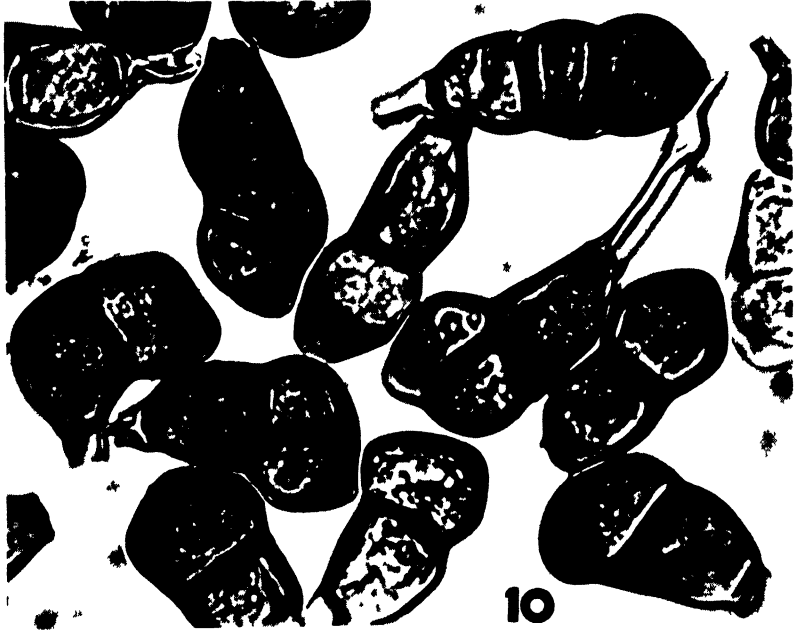
Fig. 9. Photograph of a group of teliospores of *Scopella lucumae* (stained). The outer portion of the pedicel being hygroscopic swells and dissolves leaving only a slight collar next the spore. ×800.

Fig. 10. Photograph of teliospores of *Puccinia poikilospora*. In addition to the two- and three-celled spores, four-celled spores with the same conformations also occur commonly. ×750.

The telia described here were found in old uredial infections on *Bauhinia heterophylla* Kunth, collected March 25, 1919 at Canasi, Prov. Matanzas, Cuba, by J. R. Johnston.

This interesting species is especially distinctive because of the swollen pedicels of the teliospores. After soaking in water the outer portion appears to dissolve, or at least becomes invisible, while the central strand maintains the connection between the spore and the basal cell. The basal cells are free in their upper portion and attach below to a large-celled tissue three or more cells in thickness. Hyphae of large diameter (4–6μ) branch off from the innermost boundary of the cellular layer and are easily observed in the tissue of the leaf.

During my study of *S. bauhiniicola* I examined a specimen on *Lucuma cainito*, vicinity of Para, Brazil, May 15, 1908, *C. F. Baker*. This rust was determined by Dietel as *Uromyces lucumae* Diet., and what is probably the same collection was issued in Sydow Fungi exot. exs. *6*. The teliospores (fig. 9) of this rust are strikingly similar to those of *S. bauhiniicola* in size 14–19 $\times$ 38–54μ) and also have hygroscopic pedicels whose outer portion dissolves away. Usually the only indication of the nature of this outer portion is a persistent collar-like remnant attached to the spore. The persistent central strand resembles that described for *S. bauhiniicola*.

Unfortunately, I have been unable to observe satisfactorily the basal attachment of the pedicels of *Uromyces lucumae*. Several spores may attach to an irregular and rather large basal cell but there seems little evidence that the basal cells are elongate or laterally free and they may be components of a cellular hymenium. If this is true the cells of the hymenium are larger than in other species with which I am acquainted.

The taxonomic status of *U. lucumae* is open to question. If the basal cells can be demonstrated to be laterally free it belongs in the genus *Scopella* but if the basal cells are in reality components of a compact cellular hymenium it belongs in the genus *Maravalia*. Basal cells, as other morphological structures, are presumably subject to considerable variation. There is no rule by which one can definitely decide when basal cells cease to be basal cells and become parts of a cellular hymenium. This question does not arise in connection with the highly developed basal cell of *Scopella echinulata* (Niesel) *Mains*. It begins to enter when one studies *S. cryptostegiae* and *S. bauhiniicola*, however. Knowledge of the pycnia and aecia of these species would help to clarify the situation.

Because of the marked similarity between *Scopella bauhiniicola* and *Uromyces lucumae* Diet. the latter is here transferred to the genus *Scopella* as **Scopella lucumae** (Diet.) comb. nov. (fig. 9).

Uredo wakensis sp. nov.

Uredia amphigena, subepidermalia, dense aggregata in maculis 1–3 mm. diam., pulverulenta, cinnamomeo-brunnea; urediosporae obovoideae vel globoideae, 19–23 × 21–26μ; membrana 1.5–2μ cr., cinnamomeo-brunnea, moderate echinulata, poris germ. 2, aequatorialibus.

On *Tournefortia* sp., Wake Island (taken at Honolulu, Hawaii, Feb. 22, 1938 by A. M. Mito as number 12603. Communicated by Dr. J. A. Stevenson). Type specimen in the Arthur Herbarium, Purdue University Agricultural Experiment Station and in the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

The closely aggregated uredia occupy slightly hypertrophied spots and have the appearance of uredinoid aecia but no pycnia were found by sectioning.

PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION

Conidial Germination of the Cotton Root-rot Fungus *

Elizabeth Ojerholm Roberts

The conidia of the root-rot fungus, *Phymatotrichum omnivorum* (Shear) Duggar, which are produced in large numbers on the soil surface, have been the object of studies by Duggar, Taubenhaus and Ezekiel, Peltier and King, and others. Spore cultures would extend our knowledge of the life history of the fungus and offer some promise of the development of control measures. Germination under various culture conditions has been reported to occur sparingly or not at all, and the growth resulting from germination to be limited and transitory.

Fresh conidial mats were collected from various localities in Texas and Arizona and used immediately or stored under one of the following conditions: 5°C for three days or more, room temperature for varying periods, room temperature followed by three days or more at 5°C. For testing, fresh or stored conidia were treated with mercuric chloride solution and placed in plate or hanging drop cells for germination counts. Various decoctions and synthetic media were used at different temperatures, light intensities, and atmospheric compositions, and in the presence of living cotton tissue.

Maximum germination of conidia, which never exceeded 5 per cent, occurred when they were incubated at a temperature of 30°C in darkness for three days after the fresh material had been stored at a temperature of 5°C. Spores that had been stored at room temperature for several months and failed to germinate developed germ tubes after storage at 5°C. It is obvious from this that dormancy rather than non-viability may account for the failure of the spores to germinate. Germination took place at 30°C in the following media: egg albumen agar, potato dextrose agar, Weindling's agar, potato dextrose and manure decoction broth, potato dextrose agar + yeast extract, potato dextrose agar + manure. These media were equally favorable for spore germination. Germ tubes frequently reached a length of 34 microns, or five to seven spore diameters, considerably longer than those figured by Taubenhaus. The duration of the germ tube averaged three days.

Other incubation conditions and other media showed reduced or no germination. The addition of 10 per cent carbon dioxide to the atmosphere checked all germination. No germination was obtained on silica gel to which was added nutrients or on black soil mixed with a solution of glucose

and K_2HPO_4. After passage through the alimentary tract of earthworms, spores failed to germinate. Spores did not grow in decoctions of bind weed, leaf mold, soil, cotton root, and in Waksman's agar, and in agar $+$ 5 per cent sorghum molasses. Extract media prepared from ground yeast and filtered broth cultures of yeast, *Fusarium sp.* or *Trichoderma lignorum* did not induce spore germination. Attempts to induce germination of the spores on living tissue of cotton, bind weed, potato, and carrots failed. Volatile substances given off from the cotton plant tissue had no effect on germination. Germination was not improved by contact with *Phymatotrichum* hyphae according to the method of Ferguson.

The failure of the germinated conidia to continue development may be explained by the assumption that the fungus is heterothallic and that cultures so far tried contain but one of the necessary plus and minus strains. Mixed cultures were seeded with conidia from different localities without prolonging the period of growth or resulting in anastomosis.

The conidia of the cotton root-rot fungus may remain viable for considerable periods of storage at room temperature and be induced to germinate by appropriate treatment. The low percentage germination observed is doubtless in part due to the treatment with mercuric chloride solution. Although the development of the germ tube is extended by incubation at 30°C it is strictly limited. Whether exacting culture requirements or failure to secure mixed cultures of heterothallic strains is responsible for this has not yet been determined. The growth of the germ tube furnishes an identification check, since growth of Phymatotrichum is limited and that of contaminants is not.

CLAYTON FOUNDATION
  DEPARTMENT OF BOTANY AND BACTERIOLOGY
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      AUSTIN, TEXAS

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Mention the BULLETIN

The Sterility of Sparks Aconite

WILLIAM JOHN BONISTEEL

(WITH PLATES 9–12 AND FIVE FIGURES)

The aconite horticulturally known as Sparks Variety has been propagated exclusively as a clone. In all the years since its introduction in 1898 there has been no record that any member of this clone has ever produced seed. The studies here reported have been made (1) to test this sterility in respect to seed formation by controlled and adequate pollinations and (2) to determine by cytological methods the conditions in sporogenesis which are involved in the abortion of pollen.

THE HISTORY, TAXONOMIC STATUS AND DESCRIPTION OF SPARKS ACONITE

This clone was introduced by Messrs. Maurice Pritchard about 1898 (10). It was obtained from a garden in Hampshire, England, and named after a gardener on the nursery staff whose name was Sparks. Sparks Aconite is widely grown and listed in horticultural literature. Standardized Plant Names (11) lists this clone as "Sparks Aconite (Hort. var. of *Aconitum napellus*)." Nursery catalogs list this clone as "*Aconitum napellus*, Spark's Variety," but it is certain that all plants of this type constitute a clonal variety. This clone has been considered a hybrid but no one has adequately related this clone to any species as parents. Gáyer (5) in his taxonomic treatment of European aconites makes no mention of Sparks Aconite. I know of no adequate description of this clone in the literature. Since there is evidence that this aconite is not a true species but only a horticultural clone, I shall refer to this clone as Sparks Aconite. It should be noted that Schafer and La Cour (10) consider that this clone may be a hybrid or one of several hybrids and they note that the taxonomy and origin are not definitely known.

The stem of Sparks Aconite is herbaceous, erect, branching, terete, glabrous and from 7 to 11 millimeters in diameter. It has a height of 1 to 1.5 meters under good cultural conditions. The leaves are alternately arranged on the stem and they are single, petiolate, glabrous, and lacin-

ately divided. The leaves on a single stem are few in number and seldom more than ten are present.

In the genus *Aconitum* specialization of floral structures extends to the essential organs of the flower itself. Important characteristics are also found in the underground portions of the plant. Schafer and La Cour (10) have divided the genus *Aconitum* into three sections, based upon the underground nature of the tubers and roots. The first, of which only one species is known, is represented by the annual *A. gymnandrium* Stapf. The second section, LYCOCTONUM, has perennial rhizomes and contains approximately 25 species or clones. The third section, EUACONITUM, is characterized by tubers and various shades of blue flowers and is represented by approximately 150 species or clones. A subsection of this last group includes *A. anthora* which has tubers but differs in that the petals are persistent.

Sparks Aconite belongs in the EUACONITUM section but differs from all the species or other clones of the section in great vigor of growth especially exhibited by the large number of daughter tubers that are produced. As many as thirteen may be present at one time, all attached to a single mother tuber. Especially is this in marked contrast to many other aconites that produce but one or at the most three daughter tubers annually for a single mother tuber.

The inflorescence of this clone is a raceme developing as a cymose panicle below. The terminal flower cluster with an average of nine flowers is the first to bloom. From eight to twelve lateral branches arise from the main stem and these are further sub-divided. After the terminal branch blooms the laterals continue the flowering in their descending order. Thus there is a continuous shed of pollen for almost the entire blooming period of any plant.

More than 25 per cent of the flower buds are aborted. Bud abortion is greatest in certain sub-lateral branches but may affect a series of three or more flowers placed elsewhere. These buds wither but do not drop from the floral branch until the entire period of flowering is over. This condition is typical of Sparks Aconite. Plants of this clone were grown in various soil and moisture conditions. The extent of the abortions of flowers is quite the same for plants grown in dry, in semi-dry and in various grades of moist soils. This condition seems systemic for Sparks Aconite and seems not to be related definitely to moisture in the soil. Yet a considerable proportion of normal flowers always develop. Peloric flowers are found occasionally in most of the plants either as a terminal or a basal flower in an individual inflorescence. Nectaries are seldom present in these flowers, or, if present, they are so abnormally placed as to be of little or no benefit as far as insect visitation is concerned.

In Sparks Aconite outstanding vigor is seen in the large number of flowers which are produced. A well grown plant will have an average of 150 flower buds on a single flower stem. No other member of the EUACONI-TUM group has such a large number of flowers. The flowering period of a single stem extends from 35 to 45 days. Individual flowers persist for a period of seven days. These flowers are deep blue in color and when compared with Ridgway's color chart are designated as Bradley's violet.

The pistils of the well developed flowers of Sparks Aconite appear normal for some days after the pollen is shed whether there is pollination or not. The carpels increase in size but the ovules wither in two days after the pollen of the individual flower is shed. Aborted pistils are frequently found. Examination shows that the ventral sutures of many of the carpels are not closed in which case the ovules may be exposed. Examination of serial sections shows that many of the sutures in young carpels have gaps of varying degrees. These sections also show at times the presence of accessory but poorly formed anther sacs formed in the wall of some of the carpels, but none of these dehisce to shed microspores. Normal secretion is present upon the stigmatic surfaces when they are fully expanded and it persists for two days.

The flowers of the clone may open at any time of the day or night and one or more stamens will be found shedding pollen at the time when a flower opens. Progressive shedding of pollen occurs until all of the 50–56 anthers have dehisced. The complete period is about four days. Somewhat less than 24 hours elapse after the last pollen discharge before the stigmatic lobes of the 1–3 carpels in each flower are open. When pollen, as it often does in selfing, falls upon the unopened stigma it is pushed aside when the stigma unfolds later. This is a matter to be especially considered in making proper hybridization crosses. There is a succession of anthers in dehiscence varying over a period of four days but the last pollen for a flower is shed before the pistils of that flower seem to mature.

All aconites show some degree of dichogamy. In Sparks Aconite protandry is complete for all flowers that open and self-pollination is apparently not possible. The individual flowers shed pollen for a period of four days; then a period of nearly 24 hours occurs before the pistils are receptive. With a succession of flowers the number of flowers that is open at the same time fluctuates and for a considerable period of time, especially during the middle of this blooming period, there is chance for close-pollination so that it is possible for the proper pollination of many flowers. Hence the condition of dichogamy is not responsible for the complete and continual failure of seeds to form for any of the flowers.

It can be concluded that aborted flower buds, peloric flowers, and pistil abnormalities act together to reduce seeding. But in respect to

dichogamy (12) there are numerous flowers which appear normal and there is opportunity for proper close-pollinations or for proper intra-clonal pollinations especially when there is a group of individuals in flower. Hence the conditions operating to effect the complete sterility of seed production are to be sought in the nature of the spores and germ cells.

<div align="center">EXPERIMENTAL TESTS FOR SEED PRODUCTION</div>

Pollinations were made to determine whether the pistils and ovules of Sparks Aconite are able to yield seeds to any kind of pollinations. Controlled pollinations were made with the use of glassine bags. The flowers involved were emasculated just prior to their opening. It is necessary to remove the nectaries since ants prove troublesome and can effect pollination through visits from plant to plant. We may note that these precautions, while advantageous in controlled hybridizing pollinations, were not involved in this experiment since seed was never set to any kind of pollination.

A total of 451 close-pollinations were made over a total period of three years. Plants of the clone from seven different sources were used. A total of 181 intra-clonal-pollinations were made. As will be reported later, pollen germination tests revealed but one-half of 1 per cent viable pollen. Since the pollen of one anther of Sparks Aconite contains between 300 and 500 pollen grains, one should expect at least two or three good grains to be present in the pollen applied yet in.no case was a seed set.

Hybridizing pollinations were made with pollen of approximately 50 different aconites. Many of these plants were known to produce pollen that is highly viable. No ovules of Sparks Aconite functioned in the setting of seed to any of these hybridizing pollinations.

Observations on plants of Sparks Aconite which grew in a breeding plot beside various other clones and species of aconites with abundant opportunities for open-pollinations have been made for a period of several years. In no instance has a single capsule or seed been formed on any plant of Sparks Aconite. From correspondence and observations in nurseries I find no evidence that seed has ever been produced by plants of this clone.

Utilizing the same aconites that were used in pollinating Sparks Aconite, viable seeds were obtained from over 75 hybridizations. The crosses involved plants of varieties regularly producing viable seed and included diploids, tetraploids and many clones that were triploids. Numerous hybridizations failed. Of the many species used as parents in these hybridizations some plants set seed to close-pollinations. Studies of the pollen of these indicate varying degrees of pollen abortion but for most authentic species pollen viability was high and seed production frequent.

Thus, in the numerous controlled pollination experiments plants of Sparks Aconite have produced no seed to any pollination either close-pollination or hybridizing pollination.

THE CHROMOSOME NUMBERS FOR THE GENUS ACONITUM

The somatic chromosome numbers reported (1, 2, 8, 10) for somatic tissues in members of the genus *Aconitum* are 16, 24, 32, 48 and 64. These numbers suggest that the basic number is 8. The section LYCOCTONUM (mostly yellow or purplish flowered) which is not discussed in this paper, have, it appears, only 16 chromosomes. The EUACONITUM section in which the Sparks Aconite evidently belongs has all the numbers indicated above.

The species of the EUACONITUM section which possess 16 (2n) chromosomes are usually known only as wild plants and include *Aconitum paniculata; A. variegatum; A. volubile latisectum; A. noveboracense* (reported here for the first time) ; *A. heterophyllum; A. toppinii; A. transectum; A. Forrestii; A. excelsum; A. yugapense; A. Hemsleyanum; A. barbatum;* and *A. volubile.*

The aconites with 24 chromosomes are commonly cultivated. It is possible that some are representatives of wild species but it is certain that others are only horticultural clones. Of these types those which are reported to have a somatic number of 24 (3n) chromosomes are: *A. Stoerkianum* (8 clones investigated by Afify (1), Schafer and La Cour (10) ; *A. napellus; A. variegatum;* and Sparks Aconite. Although some of these have been called species it may be that they consist of one or more clones each.
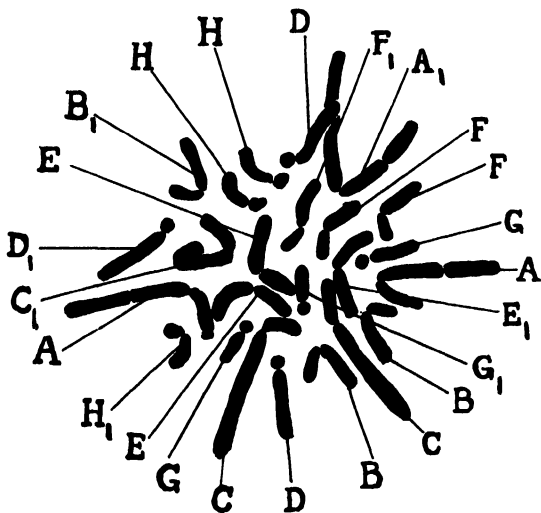
Fig. 1. Somatic chromosomes from the root tip of Sparks Aconite. (3n = 24) Chromosomes identified as A, A and A_1; B, B and B_1; etc.
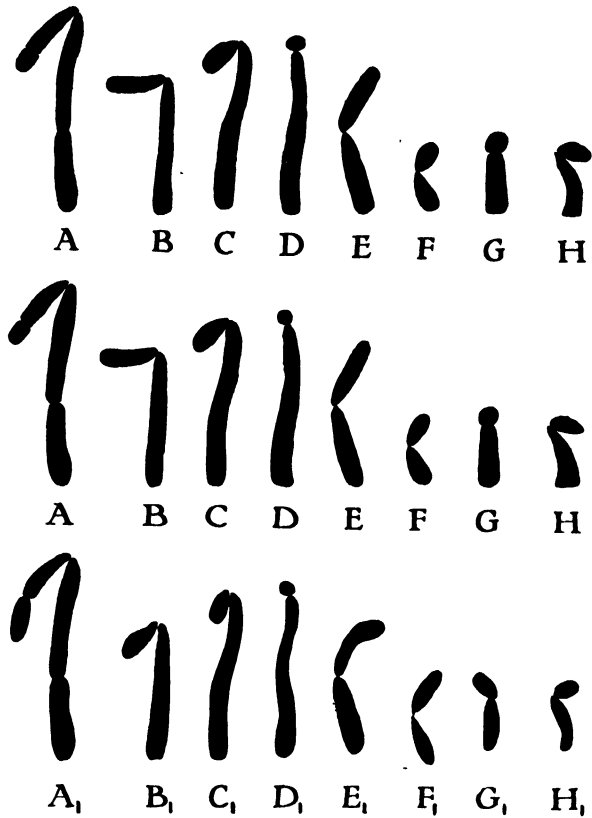
Fig. 2. Semi-diagrammatic drawings showing the relative size and shape of the three sets of eight chromosomes each in root tips of Sparks Aconite. The two *A* sets are alike while A_1 set differs in certain points as indicated in the description. The descriptions of the chromosomes of Sparks Aconite is as follows:

A and A; 6.3 microns long; median or sub-median constriction; shorter arm constriction with a knob at tip; long arm secondary constriction.

A_1;   Shorter arm constriction has an extended knob at tip.

B and B; 4.2 microns long; sub-median constriction; shorter arm constriction at right angles.

B_1;   Shorter arm somewhat bulbous and depressed.

C and C; 5.3 microns long; sub-terminal constriction; terminal knob bent over.

C_1 Terminal knob appears compressed against the long arm.

D and D; 5.3 microns long; terminal constriction; erect terminal knob.

D_1 Smaller terminal knob and slight twist to long arm.

E and E; 2.5 microns long; median constriction; arm at slight angle.

E_1;   One arm longer with a slightly twisted knob at apex.

F and F; 1.4 microns long; median constriction; short chromosomes.

F_1;   Slightly elongated and not so compact.

G and G; 1.8 microns long; sub-median constriction; erect terminal knob.

G_1 Knob elongated and bent over.

H and H; 2.1 microns long; sub-terminal constriction; terminal knob bent over.

H_1;   Knob more erect.

The species or clones which have a somatic number of 32 (4n) chromosomes are: *A. chinese; A. spicatum; A. napellus* (13 clones) (10) ; *A. Californicum; A. Delavayi; A. Kusnezoffi; A. volubile; A. anglicum;* and *A. paniculata.*

The only species reported which has the somatic number of 48 (6n) chromosomes is *A. palmatum.*

Species or clones reported which have a somatic number of 64 (8n) chromosomes are *A. Wilsoni, A. volubile latisectum* and *A. Delavayi.*

It is of special note that the following types have been reported as having two or more different chromosome numbers:

A. paniculata	16 (*10*)	24 (*10*)	32 (*10*)	......
A. variegatum	16 (*10*)	24 (*6*)	32 (*10*)	......
A. napellus	......	24 (*6*)	32 (*10*)	......
A. Delavayi	......	......	32 (*6*)	64 (*10*)

It is clear either that these plants were improperly identified or that polyploidy has occurred within the species, or that a mixture of types is present in the species.

In my experiments controlled pollinations show that many of these species or clones hybridize freely. However authentic material for breeding experiments can only be obtained from wild stocks or from cultivated plants evaluated by adequate study. Living plants are listed under various names many of which are unreliable. Seeds obtained in the open market give progeny that are variable and from one lot of seed three or more types have been grown. Seeds collected in mixed plantings of species and clones as grown in gardens especially in botanical gardens are liable to yield hybrids.

CYTOLOGICAL STUDIES OF SPARKS ACONITE[*]

1. Chromosomes in Somatic Tissues

(*a*) *Triploid number of (3n=24) chromosomes.*—The rule in the somatic tissues of root tips in members of Sparks Aconite is 3n=24 chromosome. This agrees with Langlet (6) and Schafer and La Cour (10). These chromosomes fall into three groups of eight each for it is possible to identify 8 pairs which are alike while each of the third set differs only slightly (text fig. 1).

The individual chromosomes (text fig. 2) are differentiated by total size, by the position of constriction points, and by the size of the arms.

[*] Material and Methods: The following killing and fixing solutions gave the best results with root tips: La Cour's 2 BE (7); Allen's modification of Bouin's; Chromacetic; Fleming's strong; La Cour's 2 BD; and Navashin's. Sections were cut from 15 to 25 microns and stained usually with Newton's iodine gentian or crystal-violet. Flower buds were examined in temporary aceto-carmine smears. If the desired stage of meiosis was procured the buds were placed in the killing and fixing solutions. Sections were cut

Three chromosomes, here called the A group, are similar but two of the members have a shorter arm constriction with a knob at the tip while the long arm has a secondary constriction. The third A differs from the long pair in that the knob has an extended tip. The sets of three chromosomes identified as F, G, and H are more difficult to determine. The entire complement can be resolved into AA and A_1, BB and B_1, etc. There are 8 different types of chromosomes with 3 of each type that are noticeably similar and which may be considered as homologs. The distinguishing characteristics of the chromosomes can be traced in somatic metaphases (text fig. 1 and in text fig. 3). In several preparations of root tips collected from different tubers of Sparks Aconite, cells with 6n=48 chromosomes were found along with cells which had only 24 (3n). The cells with the hexaploid chromosome number are larger than adjacent cells with triploid complements. The identity of the individual chromosomes (text fig. 3) was determined in certain of these cells. Sectors of the roots with differing chromosome numbers may be explained in the genus *Aconitum* by chromosome duplication in incompleted mitosis.

(b) *Somatic Sectors with the Hexaploid Number (6n=48)*.—In the survey of the chromosome number of the aconites it was noted that four species are listed with two or more differing chromosome numbers. Both *A. paniculata* and *A. variegatum* are listed with chromosome numbers of 16, 24, and 32. Both *A. napellus* and *A. Delavayi* have chromosome complements listed as 24 and 32, and 32 and 64 respectively. There is a question whether this material was properly identified or whether duplication

from 20 to 30 microns and stained in the same manner as root tips. Buds were preserved in a solution of one part of glacial acetic acid and two parts of absolute alcohol for 24 hours and then transferred to 80 per cent alcohol and held for further study. Belling's method for making aceto-carmine smears proved the most satisfactory. The anther sacs are very small and it was necessary to crush the anthers on a slide with pressure and to remove the anther masses before adding the stain. The early stages are not satisfactory with the aceto-carmine method since it is difficult to remove all the debris of the young anthers.

Explanation of Plate 9

The stages in microsporogenesis of Sparks Aconite.

Fig. 1. Early prophase showing two pairs of homologous chromosomes. One pair shows close homology while the other pair is loose especially at the ends. Gentian-violet. ×2000.

Fig. 2. Association of homologs at first metaphase showing three trivalents, five bivalents and five univalents. Gentian-violet. ×1400.

Fig. 3. Separation of paired homologs of bivalent association during late metaphase of the first meiotic division. Gentian-violet. ×3300.

Fig. 4. Metaphase showing irregular distribution of chromosomes. Gentian-violet. ×1400.

Fig. 5. Anaphase 1 showing lagging chromosomes and irregular poleward movement. Gentian-violet. ×1400.

Fig. 6. Anaphase 1 showing irregular grouping of the chromosomes and spindle abnormalities. Gentian-violet. ×1400.
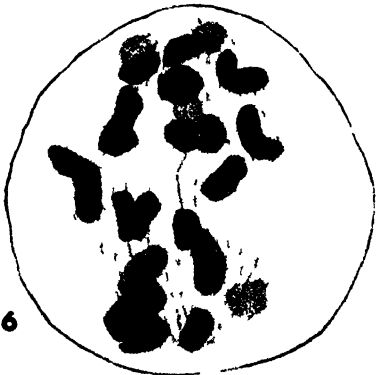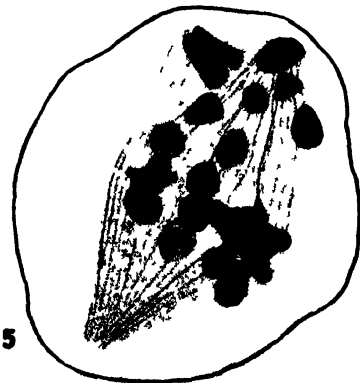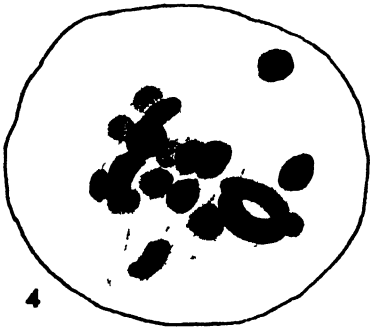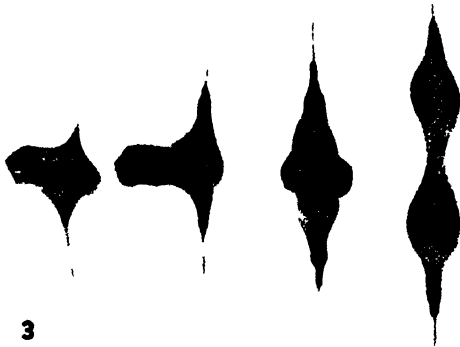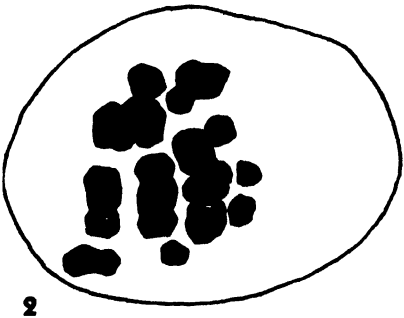
of chromosomes took place. Schafer and La Cour (10) report tetraploid sectors in the root tips of the diploid (*A. transectum*) and in a clone of *A. vulparia,* which is a species in the LYCOCTONUM group. It is obvious that hexaploid cells in the growing points of stems could develop into a sector of branches and into complete branches which could readily give rise to new types. But thus far no such branches have been observed in any member of the clone of Sparks Aconite.

2. Cytology of Microsporgenesis

(*a*) *Early Stages of Meiosis.*—In Sparks Aconite the early prophases of the first meiotic division show that 24 chromosomes as slender elongated threads in univalent, bivalent and trivalent conditions. The drawing (Plate 9, fig. 1) shows two pairs of homologous chromosomes with each pair in association. In one pair the association is loose especially at the ends, while in the other pair association is fairly close. When three chromosome threads are in association, it is the rule that two of them are more closely paired and twisted about each other, while the third thread is loosely
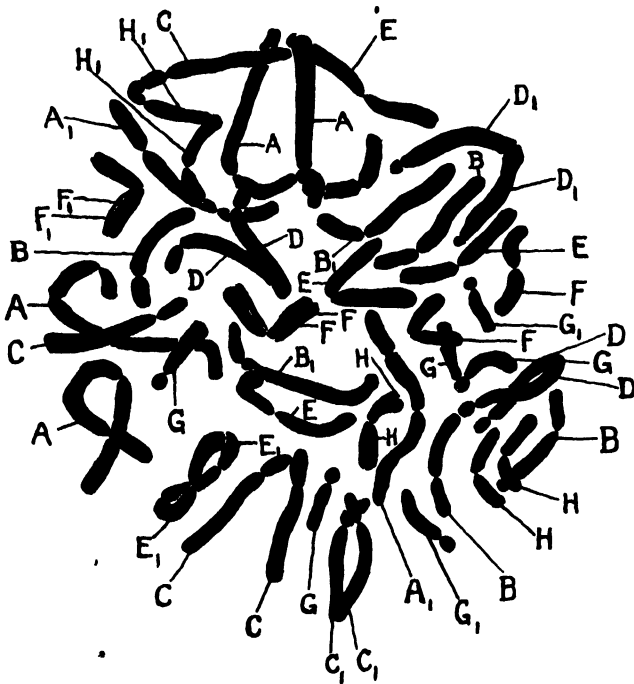
Fig. 3. The somatic chromosomes of an equatorial plate in a single cell from a sector in a root tip of Sparks Aconite in which cells have a hexaploid (6n = 48) number of chromosomes. All chromosomes were identified as indicated. Thus four A's and two A_1's are present, etc. (Compare with text fig. 1 and 2).

thrown about the other two with contacts at few points. I have observed at this stage no instances in which three chromosomes were in close association throughout their lengths. After synapsis there is a thickening and shortening of chromosomes and at the extreme contraction in the later stages the chromosomes become short and compact.

Univalents, bivalents and trivalents are found during prophase and early metaphase of meiosis. The frequency of associations was determined from a study of over 100 pollen mother cells (text fig. 4). The number of bivalents in the different cells varied from three to ten with seven bivalent associations occurring 35 times. The number of univalents per cell varied from one to ten. Four trivalents in a single cell were observed but twice. Two and three trivalents were most frequently found in cells. Two trivalents were found 35 times and three trivalents 45 times. Cells with only one trivalent were found 22 times while in a few cases trivalents were absent. The maximum number of trivalents found in any cell was four. Multiple associations of more than three chromosomes were observed in many cells. Thus two cases of quadrivalents were found together with many rings of four and chains of four, five and six chromosomes.

Thus in Sparks Aconite it is obvious that the three sets of chromosomes do not associate in trivalents with regularity. Afify (1) working with *Aconitum Stoerkianum* (3n=24) found that the trivalents varied from five to none. Cells with three and four trivalents were most frequent. The bivalents varied in the different nuclei between two and six and the univalents varied from three to eleven. This condition is not universal however for cases are known in which the complete number of trivalent association is the rule (e. g. *Datura*, Belling 1927).

The number of bivalents necessary to complete the chromosome complement was also compiled (text fig. 5) from the pollen mother cells used in the study. A solid line indicates the presence of univalents and trivalents while a dotted line indicates the number of bivalents which are necessary to complete the chromosome complement. In one case two univalents and two trivalents "2–2" were present, a total of eight, and the number of bivalents necessary to complete the complement is eight. The two or three quadrivalents are not shown on this chart. In 16 cases certain chromosomes were missing or in such a pycnotic condition that they were not recognizable.

(b) *Metaphase of the First Division.*—At metaphase there are three sets of eight chromosomes each to assemble at the equatorial plate. Eight trivalents however were never found in any cell. A somewhat typical pollen mother cell at metaphase is shown in Plate 9, fig. 2. In this case there were three trivalents, five bivalents and five univalents. The chromosomes at this stage are characterized by an extremely short and compact form and
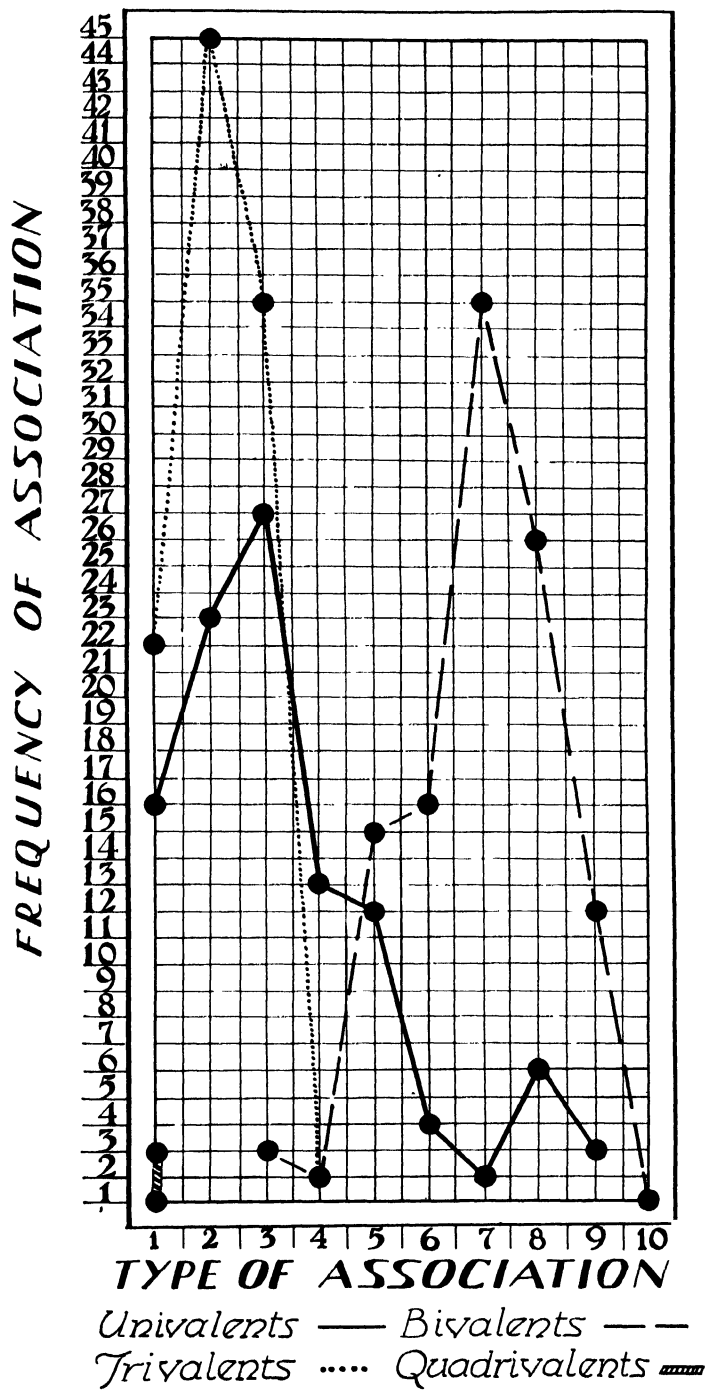
Fig. 4. Frequency of Association in the late stages of prophase of meiosis in the P. M. C.'s of Sparks Aconite. The frequency is plotted on the ordinates while the abscissas indicate the number of chromosomes which are associated.

it is difficult to identify the chromosome after such contraction. The uni-
valents, bivalents and trivalents do not lie evenly on the equatorial plate
and lagging elements are found in all material studied. Unpaired chromo-
somes are found in many of the cells while in other cases some of the
chromosomes apparently do not reach the equator but lag (Plate 9, fig.
4). Certain of the chromosomes lay beyond the range of the spindle fibers.
At late metaphase the chromosomes are dense but they may become at-
tenuated under tension (Plate 9, fig. 3) when the separation of the paired
homologs occurs.

(c) *Anaphase of the First Division.*—At metaphase lagging elements
were present and the early stages of anaphase are characterized by con-
tinued irregularities. Not only are lagging chromosomes to be observed on
the spindle (Plate 9, fig. 5) but some of the chromosomes do not advance
to the poles normally but stop half-way (plate 9, fig. 6). Chromosomes
may remain at the equator when pairs of homologous chromosomes have
separated. The general rule is that the separated chromosomes pass to the
poles without any separation of their chromatids. The compact nature of
these short chromosomes is maintained throughout the stages of first
anaphase. There is evidence that the chromosomes having terminal or
subterminal spindle attachments show arms after they have separated.
But in no case is there a tendency for the chromosomes to form V-shaped
figures as reported in the case of first anaphase in many plants. The
presence of trivalents and univalents results in irregular distribution.
Two chromosomes of a set of three may pass to one pole and one to the
other. Unpaired chromosomes may lag at the equator, some show signs of
the premature separation of their chromatids while others pass undivided
to the poles. In late anaphase examination of both aceto-carmine and

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Explanation of Plate 10

The stages in microsporogenesis of Sparks Aconite.

Fig. 1. Anaphase of the second meiotic division of Sparks Aconite showing unequal
distribution of the chromosomes to the poles, lagging chromosomes and one chromosome
outside the spindle apparatus. Gentian-violet. ×2400.

Fig. 2. Semi-diagrammatic sketch of fig. 1 in which the individual chromosomes are
lettered. Chromosome H is outside the spindle and it is evident that it does not reach
a pole. Chromosome D is stretched out as a bridge between the two poles.

Fig. 3. Diagrammatic sketch with spindles connecting three of the four nuclei. Iron-
haematoxylin. ×1200.

Fig. 4. Upper (1) and lower (11) focus showing late 2nd telophase with faint begin-
ning of cytokinesis in the form of a slight constriction at the middle of the spindle. Iron-
haematoxylin. ×1300.

Fig. 5. Incompleted furrowing. Iron-haematoxylin. ×1200.

Fig. 6. Furrowing completed showing four microspores within the wall of the
original P. M. C. Iron-haematoxylin. ×1200.

Fig. 7. Tetrads partially collapsed, a frequent stage leading to abortion. Iron-
haematoxylin. ×1200.
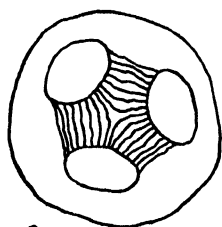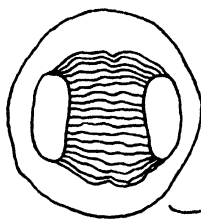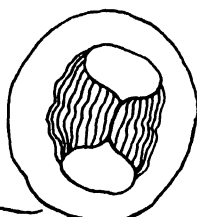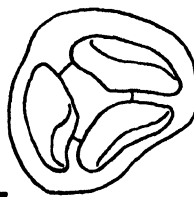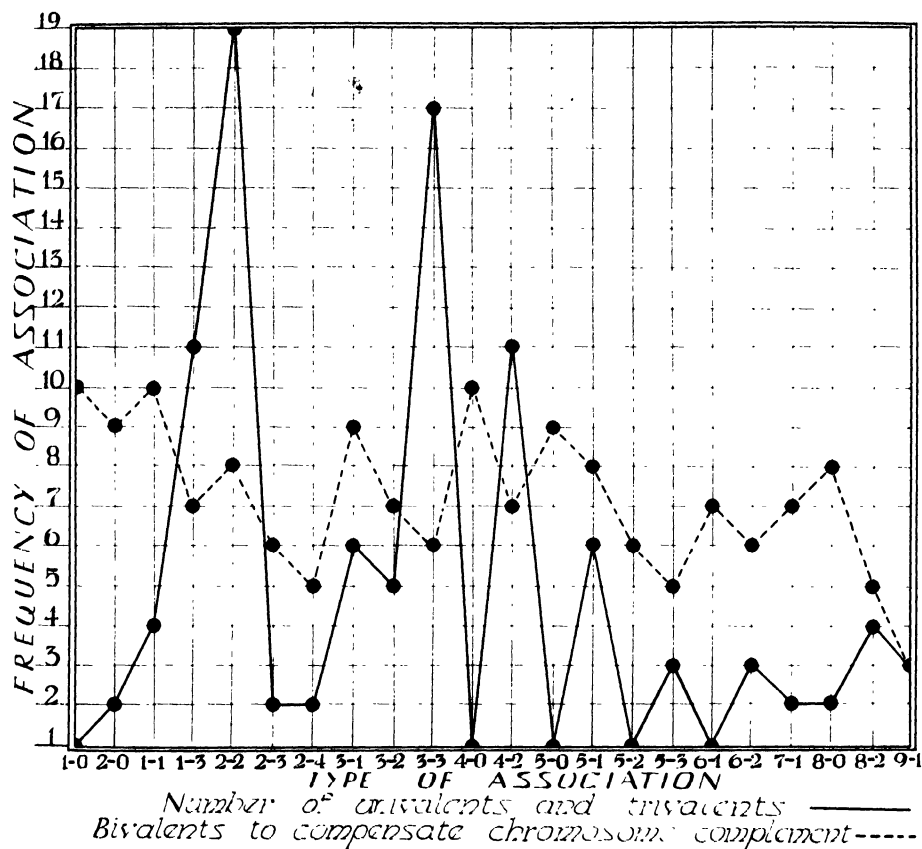
Fig. 5. Diagram indicating the number of bivalents necessary to complete the chromosome complement for the cases reported in text fig. 4 on the basis of the number of univalents and trivalents observed. The number of univalents and trivalents are indicated in the abscissas $1 - 0$; $2 - 0$; $1 - 1$; etc., in which the first number is the univalent and the second number the trivalent. Both univalents and trivalents are indicated by the dotted line. In the case "$2 - 2$," there were present two univalents and two trivalents, a total of 8 and the number of bivalents (indicated by the solid line) necessary to complete the complement is eight.

fixed preparations shows the presence of chromosome elements in the cytoplasm (Plate 11, fig. 1; Plate 12, fig. 1). Some of these chromosomal elements are either chromosomes that were outside the equatorial plate at metaphase or elements that did not move with regularity to the poles. In still other cases certain of the chromosomes are scattered in the cytoplasm. Afify (1) reports in *Aconitum Stoerkianum* (3n=24) that the first anaphase was characterized by irregularities such as lagging, abnormal trivalent separation and the erratic behavior of the unpaired chromosomes which resulted in the poles receiving an unequal number of chromosomes. In the late anaphase of Sparks Aconite chromatin bridges (Plate

12, fig. 2) are frequently found together with extra nuclear chromatin material cast in the cytoplasm (Plate 11, fig. 2). In still other cases chromatin material is present in the cytoplasm after the separated units have rounded up at the poles (Plate 11, fig. 3).

During the first anaphase stages the irregularities are as follows:

1. Univalents may lag, or may lag and then go to the poles and some may disintegrate and become lost in the cytoplasm.
2. Bivalents may lag and there is some evidence that they may fail to separate.
3. Both bivalents and trivalents may fail to separate and often form bridges.
4. In the final distribution of the first anaphase 9 to 11 chromosomes were most frequently found at a pole. Seldom was the entire complement of 24 chromosomes distributed into two groups. Extra chromatin material was usually present outside the two groups at the poles.

(d) *Telophase of the First Division.*—The individual pairs of chromatids become slightly elongated and more undulate as the two nuclei are formed. Lagging divided or undivided univalents are found in the cytoplasm. Some of the extra nuclear material rounds up and forms micronuclear structures (Plate 11, fig. 4; Plate 12, fig. 3). Part of this extra

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Explanation of Plate 11

Stages in the microsporogenesis of Sparks Aconite. From fixed or acetocarmine preparations.

Fig. 1. Late anaphase of the first division with lagging chromosomes.

Fig. 2. Late anaphase of the first division with chromatin bridge and two extra nuclear chromosomes, apparently lags at metaphase.

Fig. 3. Late anaphase of the first division with extra chromatin material lagging.

Fig. 4. Interphase showing two large nuclei and one micronucleus.

Fig. 5. Telophase at second division with chromatin bridges between daughter nuclei.

Fig. 6. Late anaphase of the second divisions with lagging chromosomes.

Fig. 7. Telophase of second division with two chromatin bridges.

Fig. 8. Telophase of second division with extra nuclear material.

Fig. 9. Telophase of second division with lagging chromatin material.

Fig. 10. Tetrads, complete cytokinesis having taken place.

Fig. 11. Tetrads with lagging chromatin material rounding up.

Fig. 12. Four microspores within an old pollen mother-cell, showing unequal nuclear and cytoplasmic division.

Fig. 13. Polyspory, showing four microspores of equal size and one microcyte. A microcyst, a lag from the first division, is present and within two other microspores a microcyst each. A micronucleus is present in the microspore at lower right.

Fig. 14. Polyspory with six microspores in which two of them are connected by a chromosome bridge.

Fig. 15. Polyspory with a supernumerary microcyte and a microcyst inside one of the spores.

Fig. 16. Polycary, showing telophase of the second division with seven nuclei connected by multipolar spindles and six extra-nuclear microcysts.

Fig. 17. Polyspory with five microspores of equal size.
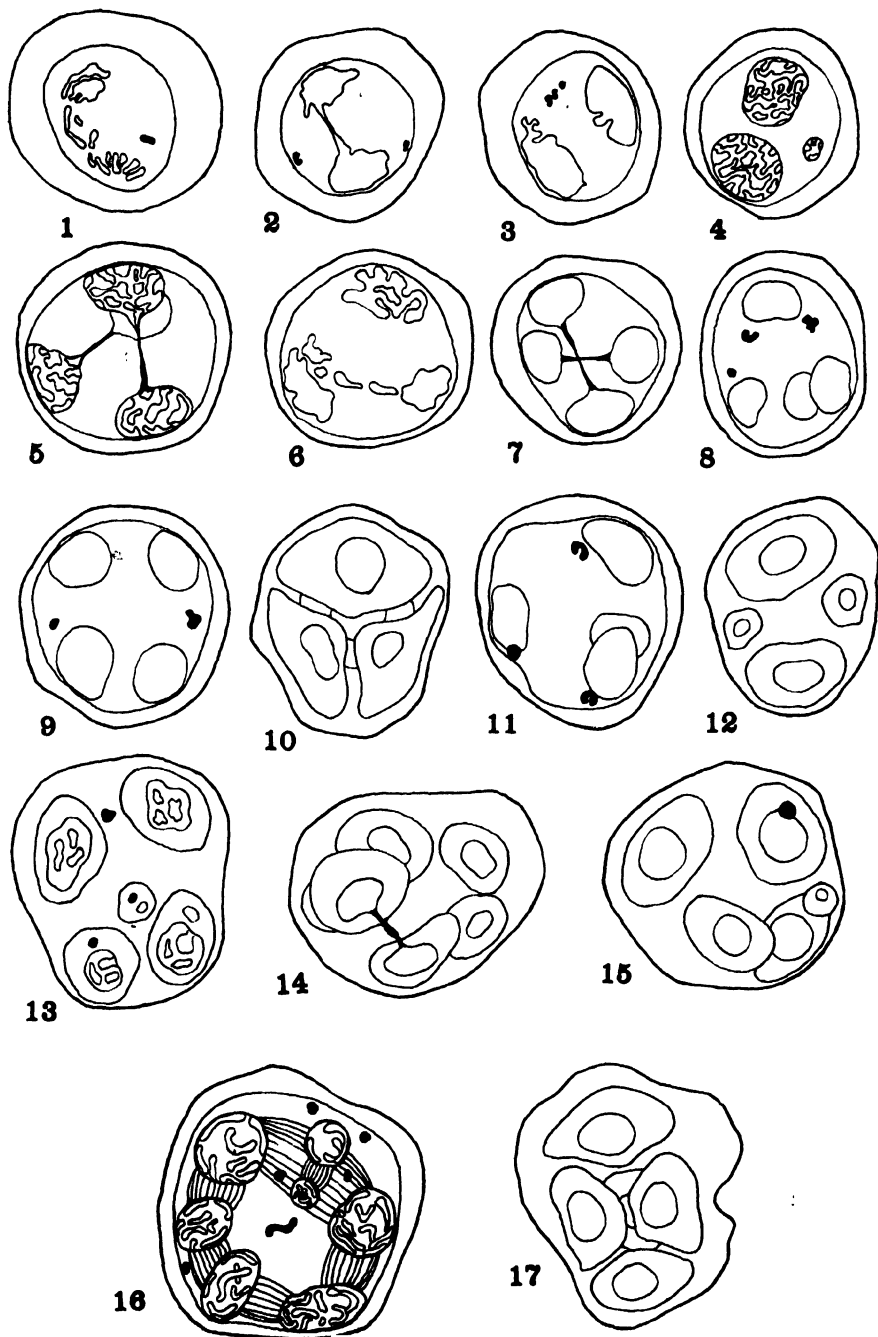
nuclear material becomes pycnotic and disintegrates during this stage or persists and disintegrates at the end of the second division.

(e) *Metaphase of the Second Division.*—The chromosomes are characterized by their irregular form and very seldom could an accurate count be made of them at this stage. Traces of nuclear fragments (whether univalents or not, could not be determined) were found near the periphery of the cell.

(f) *Anaphase of the Second Division.*—I have studied many preparations of the stages of second anaphase but have found few cases of distribution in which all of the daughter chromosomes could be identified or even counted. The chromatids separate as daughter chromosomes but many cases of lagging daughter chromosomes (Plate 11, fig. 6; Plate 12, fig. 4) and chromosomal bridges were found (Plate 11, figs. 5 and 7). Yet a study of the later stages of microsporogenesis shows that, as a rule, four large main nuclei are formed (Plate 11, fig. 10). In addition there is frequently one or more micronuclei (3) and microcytes.

One of the relatively few cases in which chromosomes were identified in the anaphase of the second division is shown in Plate 10, fig. 1. A semi-diagrammatic sketch (Plate 10, fig. 2) indicates the daughter chromosomes involved. The lagging and irregular distribution of daughter chromosomes is general for all material studied. It is to be noted that only 40 chromosomes are accounted for in this particular figure. At this stage chromosomes assume a shape and form more characteristic of the somatic chromosomes of the root tip. In this figure the distribution of daughter chromosomes shows that in one spindle there is one pole with six chromosomes while the other has eight. Lagging between these two poles are five chromosomes. One single chromosome (identified as an H) remains outside the spindle and separates from the others. Such separate chromosomes round up and either persist as microcytes or disintegrate at later stages. At the other two poles are seven and five chromosomes with eight chromosomes lagging. Notably is the chromosome D—D stretched out as a bridge between the two poles. Theoretically the total number of chromosomes should be 48 divided equally between the four poles provided that each chromatid formed and separated from its sister and that none was lost or disintegrated. It is to be noted that in the figure the missing chromosomes represent three long and two short ones. Possibly these may have been univalents of the first division that lagged and disintegrated, or perhaps extruded chromosomes (Plate 12, fig. 5) singly or in groups from the major spindle.

(g) *Cytokinesis.*—A cell plate is not formed after the first meiotic division but the four or more spores are delimited by partitions which appear at the close of the second division. For a time prominent spindles

(Plate 10, fig. 3) connect the four nuclei. At a later stage the faint begin-
ning of cytokinesis is evident (Plate 10, fig. 4, I and II) when a slight
constriction appears at the periphery in the equatorial region of the
plasma membrane. Furrows continue (Plate 10, fig. 5) to extend inward
until they reach the center and the protoplast is divided into four potential
microspores. When cytokinesis is completed the four microspores are
still retained within the wall (Plate 10, fig. 6) of the old pollen mother
sell. Farr (4) has shown in *Nicotiana* that developing furrows may cut
through any spindle fibers that may be encountered by the continued in-
vagination. Frequently at this stage one or more of the developing spores
of the tetrads (Plate 10, fig. 7) abort. Later the sporocyte wall and the
material separating the spores disappear leaving the spores free. When
pressure is applied to aceto-carmine smears at this stage the walls of the
sporocyte may be ruptured and the developing spores liberated.

   (*h*) *Organization of the Nuclei.*—The most striking condition in the
organization of the nuclei after the second division is the unequal size of
the nuclei (Plate 11, figs. 10, 12, 13 and 15) formed within a mother cell.
One or more nuclei may be full sized while the sister cells may be extremely
small (Plate 11, fig. 12; Plate 12, fig. 7). This variation in size is in strik-
ing contrast to the organization of the four sister cells in a normal diploid
plant such as *A. noveboracense*. More than four spores are frequently
found. An extreme condition of supernumerary nuclei is shown in Plate
11, figure 16, in which there were seven nuclei of various sizes with spindle
fibers radiating in the several directions of focus. Six extra-nuclear micro-
cysts were also present. Bridging of chromatin material between two
nuclei is of frequent occurrence (Plate 11, figs. 5, 7 and 14) in the later
stages of division.

   The following summarizes the principal abnormal conditions found in
the tetrad stage following the telephase at the end of the second division:

1.   The nuclei are of unequal size (Plate 11, fig. 13).
2.   One fully formed nucleus may be present while others are deficient in
     chromatin material or are collapsed (Plate 11, fig. 10).
3.   Polyspory is of frequent occurrence (Plate 11, fig. 13; Plate 12, fig. 10).
4.   Microcysts are present in one or more cells in more than 45 per cent
     of the tetrads (Plate 11, figs. 13 and 15; Plate 12, figs. 6, 8 and 9).
5.   Micronuclei are present in nearly 50 per cent of the tetrads (Plate 11,
     figs. 8, 9, 11 and 13).
6.   Lagging chromatin material is present in the cytoplasm in various stages
     of degeneration.

THE MATURE POLLEN

   From a statistical study of 250 mature pollen sacs in serial sections,
almost ready to dehisce, only 67 well formed pollen grains were observed

and 7013 grains were found that were shrivelled and more or less empty. The few pollen grains that were judged as possibly functional contained granular contents and a vegetative and generative nucleus. Both the exine and intine were well developed. Studies with viable pollen, at the same stage of development, from diploids (*A. noveboracense*, Plate 12, fig. 20, an EUACONITUM type, and *A. Lycoctonum*, Plate 12, fig. 21, a LYCOC-TONUM type) show that pollen has both a generative nucleus and a vegetative nucleus. It is to be noted that both of these diploid species set seed freely. The pollen of diploids has three germinal furrows. The relatively few grains that germinate in Sparks Aconite also have three germinal furrows but in the great majority of grains the germinal furrows are poorly developed and some pollen grains (Plate 12, fig. 14) have four germinal furrows. Many of the pollen grains (Plate 12, fig. 18) have collapsed and are of irregular size and of variable shapes. Many of the grains have scattered chromatin material and contain but little cytoplasm and in some cases there is none (Plate 12, figs. 16, 17). It is to be noted 'that

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Explanation of Plate 12

Photomicrographs.

Figs. 1–19. Triploid Sparks Aconite. Figs. 20–22. Diploid Species.

Fig. 1. Late anaphase, first division with lagging chromosomes and one lagging univalent at periphery of the cytoplasm. Aceto-carmine. ×125.

Fig. 2. Late anaphase bridge, first division, with extra chromatin material in the cytoplasm. Aceto-carmine. ×125.

Fig. 3. Interphase with one micronucleus. Aceto-carmine. ×1350.

Fig. 4. Anaphase, second division, with lagging chromosomes. Crystal violet. ×480.

Fig. 5. Telophase, second division, with a chromatin bridge and one microcyst in the cytoplasm. Crystal violet. ×480.

Fig. 6, 7, 8. Tetrad stages. Crystal violet. ×480. Fig. 6. Showing microcysts lying next to the nucleus. Fig. 7. Showing microcyte and two microcysts also next to the nuclei. Fig. 8. Showing microcysts lying next to the nucleus of upper spore.

Fig. 9. Tetrad stages with microcysts. Aceto-carmine. ×100.

Fig. 10. Polyspory with four microspores and one microcyte. Two of the microspores have an additional micronucleus each. Aceto-carmine. ×1350.

Fig. 11–17. Stages in pollen abortion. Freshly shed pollen. Aceto-carmine. ×220. Fig. 11. An ordinary pollen grain with dense contents. Figs. 12 and 13. Aborting pollen grains with chromatin content in various stages of disorganization. Fig. 14. A small pollen grain with four germ pores and one empty microcyte adjacent to it. Figs. 15 and 16. Completely aborted pollen grains. Figs. 17. One normal pollen grain in a field with four completely and three partially aborted pollen grains. Touching one of latter is a free microcyte.

Fig. 18. Microspores just prior to the shed of pollen with but one microspore capable of germinating. Crystal violet. ×220.

Fig. 19. Germination of the pollen of Sparks Aconite. One-half of 1 per cent germination. Aceto-carmine. ×80.

Fig. 20. Mature pollen of the diploid *A. noveboracense*. Crystal violet. ×220.

Fig. 21. Mature pollen of the diploid *A. Lycoctonum*. Aceto-carmine. ×220.

Fig. 22. Germination of the pollen of *A. Lycoctonum*. 95 per cent germination. Aceto-carmine. ×80.
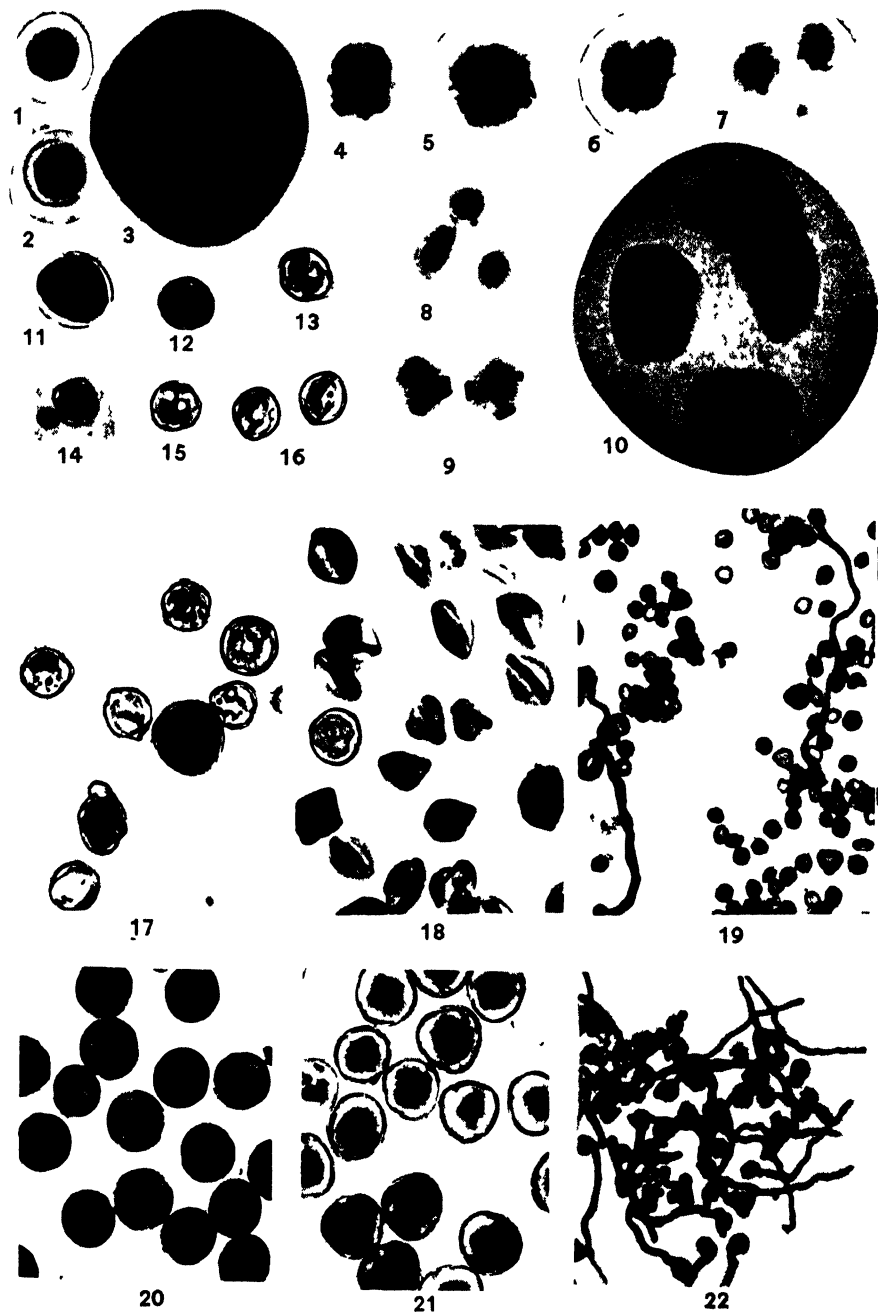
these grains (Plate 12, fig. 17) are smaller than the few potentially good pollen grains. In all species studied where the pollen functions normally in the productions of seed the content of the cytoplasm is marked. In pollen of Sparks Aconite, as is shown in Plate 12, fig. 17, it is only the very few grains which are plump and appear to be well filled with cytoplasm that will germinate if placed on artificial media. In many of the cells the chromatin material is dispersed in small rounded masses (Plate 12, figs. 12, 13 and 15), while in other cases the primary cell (Plate 12, fig. 11) does not develop further.

POLLEN GERMINATION TESTS

Pollen of a diploid (*A. Lycoctonum*) in tests for artificial germination on agar (1 per cent agar—sugar 5, 10 and 15 per cent) media gave germination of more than 95 per cent of all grains. Rarely was a collapsed or empty grain found. (Plate 12, fig. 22.)

Pollen of Sparks Aconite when tested gave an average of only one-half of 1 per cent (0.005) germination. Pollen tubes of grains (Plate 12, fig. 19) which germinated reached a length of from 300 to 1200 microns. Some of the tubes branched either soon after emerging from the pore or later.

Microcytes or small cells constitute about 5 per cent of all cells. In freshly shed pollen most of the content of these small grains has already degenerated and merely walls are present. Many pollen grains are collapsed and these grains have little granular content and lack definite pores. Aborted pollen grains constitute about 90 to 95 per cent of all grains. The aborted pollen grains are as a rule somewhat smaller than the few viable grains observed. The primary cell fails to divide in many of the spores. In other spores the presence of small nuclei indicates either unequal division of the primary cell or presence of micronuclei in various stages of degeneration. Dispersed chromatin bodies that take the acetocarmine stain were found in many spores. Degeneration is so universal in this class of pollen that many of the grains possess only walls with very little organized content. Germination of aborted grains was never observed. No increase in germination of pollen was obtained when media was used to which had been added enzymes (diastase, maltase, yeast extracts, etc.) or organic acids (citric, lactic, and malic).

SUMMARY AND CONCLUSIONS

Plants of Sparks Aconite have never been known to produce seeds. It seems certain that they constitute a clone the members of which have arisen by vegetative propagation of one original plant. Experimental tests show that the plants of this clone are unable to produce seeds with any

kind of pollination. In tests for germination only one-half of 1 per cent of the pollen germinated.

The members of this clone are triploids with $3n=24$ chromosomes. The abortions of the microspores arise in connection with the presence of three sets of chromosomes. The three sets of chromosomes function normally in the somatic tissues to produce a plant with marked vigor of growth expressed in the production of flower buds and daughter tubers. But during the complicated process of meiosis abnormalities in chromosomes behavior and distribution arise which lead to abortion of microspores. The ovules are not functional and it is probable that macrospores also abort as do the microspores.

During microsporogenesis the following abnormalities occur (1) irregular conjugation of homologous chromosomes, (2) presence of univalents, bivalents, and trivalents during the first division of meiosis, (3) irregular distribution of the chromosomes in both divisions, (4) the occurrence of polycary, (5) various abnormalities in the later stages of meiosis.

(a) In 60 per cent of the cases the three homologs of each of the eight chromosomes are not closely associated. In a similar number of cases two of the homologs are associated as bivalents without any intimate association of the third homolog. Never has there been found a case where there were either 8 trivalents or 24 univalents. It may be assumed that the bivalent associations which occur most regularly are between homologs of related origin and similar structure while the third, and usually unpaired, homolog is less similar. The irregularities of association together with the presence of three sets of chromosomes are responsible for many of the chromosome aberrations found in the various stages of meiosis.

(b) The distribution of the three sets of chromosomes in the later stages of the first division is irregular. Frequently univalents are left outside the spindle proper and many univalents do not become associated with the spindle in the equatorial plate. As the bivalents separate into their component halves and pass to the poles some univalents are left in the central part of the spindle. The lagging chromosomes may be distributed at random between the two nuclei and some form small supernumerary nuclei or microcytes. The chromatin material that is left outside of the nuclei may degenerate. The two daughter nuclei receive different numbers of chromosomes.

(c) Chromosomes continue to lag in the second meiotic division which results in incomplete distribution of chromosomes to the potential pollen grains. The microspores do not have nuclei of equal size. Micronuclei and microcysts are present in nearly all the tetrads as a result of lagging chromosomes and most of this chromatin material degenerates at a later stage. Polyspory is of frequent occurrence with as many as seven spores

formed from a single spore-mother-cell. Small spores or microcytes constitute about 5 per cent of all spores. When cytokinesis is completed the sister cells do not have their normal complement of chromosomes.

(d) Abnormalities of the microspores may be grouped as follows: (1) small pollen grains with granular contents and limited viability, (2) aborted grains with pycnotic nuclei leading to complete disorganization, (3) completely collapsed empty grains without contents, (4) small microcytes without contents and (5) microcytes which eventually disappear. The numerous chromosomal aberrations prevent the development of the pollen grains that were potentially possible.

The abnormalities which result in the abortion of pollen in the triploid Sparks Aconite are to be attributed chiefly to the presence of a third set of chromosomes. In the meiotic divisions irregularities occur in the pairing of homologs and in the distribution of the members of the three sets of chromosomes so that normal haploid sets, or other complements which may provide for functional spores, are seldom found. It is to be recognized that many irregularities such as these occur both in hybrids and in polyploids, so that such behavior of itself does not differentiate the sterility of hybrids from that of triploids. But here in Sparks Aconite the study of the structure and the character of the 24 chromosomes definitely indicates (1) the triploid nature in the presence of three sets of chromosomes and (2) a condition of hybridity.

Many of the hybrids obtained in these hybridization experiments have already produced flowers. None of the hybrids obtained thus far closely resembles Sparks Aconite. Crosses between clones or species of a decidedly branched habit have resulted in plants that somewhat approximate the branched habit of Sparks Aconite. The species or clones from Asiatic sources, known as *A. formosum* and *A. Forrestii* have in addition to the terminal flower cluster 5–6 lateral branches each bearing 6–8 flowers. These plants readily crossed with European clones and species of the section EUACONITUM and some of the hybrids were branched and showed varying degrees of sterility. Sparks Aconite has 8–12 lateral branches, each of which is often further subdivided. This condition suggests the possibility of origin by hybridizing which involves Asiatic species of the EUACONITUM section with combinations of certain species not used in these experiments.

In respect to sterilities in certain other aconites Afify (1) states that "diploid *Aconitum* species are sterile although pairing in them is regular, and tetraploid species are also sterile, showing regular pairing as well." Such a condition certainly is not to be expected for the members of any true species, especially of simple diploids, which exist as numerous individuals reproducing by seed, as a true species does. The diploid "species"

to which Afify refers are *Aconitum Lycoctonum* (2n=16), *A. orientale* (2n=16) and *A. luridum* (2n=16). Plants of the first two of these species have regularly set seed during the period of these experiments. *A. noveboracense*, a diploid endemic species of the Catskill mountains, regularly sets seed in the wild so it is not necessarily the case that diploid aconites are sterile.

Afify also studied *A. Stoerkianum* which he described as a triploid and he noted that this so-called species was thought by the systematists to be a hybrid between *A. variegatum* and *A. napellus*. Yet Reichenbach (9) described this plant as producing seeds. *A. Stoerkianum* has also been described as a tetraploid, a fact noted by Afify. Some of the plants of the so-called species described by Afify as sterile diploids may be hybrids between diploid species which have the sterility of hybridity and which must be propagated as clones.

It is certain that Sparks Aconite is a triploid with a somatic number of 24 chromosomes which are to be resolved in three sets. That it may be allotriploid in nature is suggested by the fact that two sets of chromosomes are more nearly alike. Yet the third set is not extremely different. This plant is evidently a hybrid and it could have arisen from (1) two diploid species after a fertilization in which one gamete was unreduced, or (2) one of its parents may have been a tetraploid (or a double diploid) and the other a diploid. In the recent terminology it is considered to be triploid of hybrid origin and according to the terms proposed by Warmke and Blakeslee it would be called a triple haploid.

The writer wishes to express his gratitude to Dr. A. B. Stout under whose directions these studies were carried out and for the opportunity afforded me in carrying out these investigations at the New York Botanical Garden, an affiliate of Columbia University.

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A New Species of Cordaites from the Pennsylvanian Strata of Iowa

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(WITH SEVEN FIGURES)

Abundant petrified plant material in the Pennsylvanian coal balls of Iowa has been found and is being investigated by the authors. Some Iowa specimens, which include calcified stems, roots, and leaves of *Cordaites*, were collected in an open pit coal mine at What Cheer, Iowa. The material is from the Des Moines Series of the Pennsylvanian System. Thin sections and nitro-cellulose peels of the specimens were prepared and used in the present paper.

While a number of cordaitean woods have been described from various parts of the world, relatively few are well known in America. In many of the woods there is an absence of primary structure which makes generic determination difficult.

Two stems have been studied from the above locality and these measured about 20 cm. in length and 10 cm. in diameter. The pith region, about three centimeters in diameter, has almost entirely disappeared, and this region now contains several stigmarian rootlets. The pith region is surrounded by a woody ring three to four centimeters in thickness, and bark tissues are not present.

Transverse sections of the specimens indicate a gymnospermous wood with indefinite zones which superficially resemble growth rings (Fig. 1). Under microscopic examination, these zones are found to be the result of collapsing of indefinite layer of cells.

As far as could be determined, the bordered pits of the secondary wood are restricted to the radial walls. The first pits of the tracheids are arranged in several rows, while those of the remainder of the secondary wood are in single rows. The pits occurring in single rows are generally larger than those occurring in many rows, with the former measuring about 10.95μ in width, and 7.30μ in height; while the latter measure about 8.62μ in width and many are less than 7.30μ in height.

The tracheids seen in tangential sections ranged from 14.60μ to 54.75μ in width. The majority being 35μ wide. In transverse section they are oblong in shape (Fig. 2).

The small, narrow rays vary in height from one to ten cells, the greatest number being two cells high (Fig. 5). The cells are mostly higher than wide, and the cross diameter is about half that of a tracheid. The rays are mostly uniseriate, but several biseriate rays have been observed (Fig. 5).

Fig. 1. Coal ball sectioned to show transverse structure of cordaitean stem and leaves.

Fig. 2. Transverse section of stem through the primary and secondary xylem.

Fig. 3. Radial section showing contact of sclariform and pitted tracheids.

Fig. 4. Radial section through secondary xylem showing longitudinal view of wood ray and uniseriate pitting on the tracheids.

Fig. 5. Tangential section through secondary xylem showing tranverse sections of uniseriate rays and one biseriate ray.

Fig. 6. Transverse section of *Amyelon*, a cordaitean root.

Fig. 7. Tranverse sections of cordaitean leaves.

As the rays approach the pith they broaden gradually, becoming narrowly fan-shaped. As a result, the xylem between the rays becomes narrowed to a point at the contact with the pith (Fig. 2). It is largely upon this anatomical character, the presence of a large pith surrounded by a thick zone of secondary wood of the *Dadoxylon* type, a small amount of centrifugal primary wood, and the absence of leaf traces that might designate *Mesoxylon*, that the specimens have been assigned to the genus *Cordaites*.

A review of American and European literature shows that the specimens collected in Iowa evidently represent a new species, which appears to be most closely related to *C. michiganensis* Arnold (1). In contrasting the Iowa fossils with the Michigan, the following characters have been noted:

Cordaites michiganensis Arnold	*Cordaites iowensis* sp. nov.
Tracheids regular, average diameter 35μ.	Tracheids regular, average diameter 35μ.
Bordered pits in secondary wood mostly in 2 rows, height and breadth equal.	Bordered pits in secondary wood mostly in 1 row, wider than high.
Rays low, seldom more than 10 cells high.	Rays very low, seldom more than 7 cells high.
Rays only slightly narrower than tracheids.	Rays usually only half as wide as tracheids.

Associated with the stem remains in the coal balls are abundant leaf fragments of *Cordaites*. These are not sufficiently well preserved to warrant description at present (Fig. 7). In addition a small root was found that can be assigned to the genus form *Amyelon* (Fig. 6).

Since the Iowa fossils do not agree closely with any of the American cordaitean forms described by Arnold (1), Dawson (3), Penhallow (6), and others, nor do they agree with any European forms, it appears advisable to describe them as a new species.

Cordaites iowensis sp. nov.

Pith large, primary wood narrow and surrounded by a thick zone of secondary wood of the *Dadoxylon* type. Tracheids from 14.60μ to 54.75μ in width, average 35μ, oblong in tranverse section and are fairly regular in size. Bordered pits arranged in multiple rows in the first several tracheids possessing them, and in one row in the succeeding tracheids, all slightly vertically flattened. Rays narrow, very low (1 to 10 cells, usually 2), scattered, uniseriate or rarely biseriate. Ray cells slightly higher than wide, and in width about half the cross diameter of the tracheids. Rays broadening as they approach the pith, dividing the centrifugal primary wood region into wedge-shaped segments.

HORIZON: Des Moines Series, of the Pennsylvanian System. Locality, What Cheer, Keokuk County, Iowa. Holotype in the collection of the

senior author, No. 4616, and slides have been deposited in the collections of the University of Michigan and Illinois Geological Survey.

The authors wish to express their appreciation for the helpful suggestions of Dr. C. A. Arnold.

COE COLLEGE
    CEDAR RAPIDS, IOWA

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Gallatin Petrified Forests[1]

P. A. Young

(WITH ELEVEN FIGURES)

Tall, yellow petrified logs and stumps protruding vertically from the ground were examined by the writer from 1926 to 1934 on peaks and high ridges of the Gallatin Mountain Range near the northwest corner of Yellowstone National Park (Figs. B,C,F,J,K).[2] Although most of the petrified trees were yellow or brown, a few of them were white, and some pieces of petrified wood were green or black. One white tree showed many small fragments each with only 1 to 5 annual rings, as they were petrified only enough for preservation. One tree hung from the roof of a cave, while the end of another tree trunk was in the wall of a cave. A few tree trunks were inclosed in quartz cylinders (Fig. E), and incrustations of quartz were found on several petrified logs. Many of the petrified trees showed roots, limbs, and bark-like material. Some horizontal logs were found, one of which protruded from both sides of a mountain ridge. Typical specimens of the petrified wood were identified as *Sequoia magnifica* Knowlton by Dr. R. W. Chaney of the University of California. Leaf impressions resembling those of fern, pine, redwood, elm, willow, and magnolia, and a pine cone with seeds were found in the rocks near the fossil trees.

Based on available evidence and preferable theory, the geological history of the Gallatin Petrified Forests is vizualized as follows. A forest predominating in *Sequoia magnifica* grew on nearly level land in a warm, humid climate near a Cretaceous sea.[3] Finally, volcanoes erupted ashes and rocks that broke the limbs from the trees and buried the forest with many of the trunks and stumps standing where they grew. Land subsidence soon placed these trees in a stratum permeated with hot water nearly saturated with silicon dioxide. This petrified the wood enough to preserve it well but left unchanged much of the detailed structure of most of the specimens seen, as they showed prominent annual rings (Fig. G). Petrification probably replaced the wood with silicon dioxide. All of the material solidified into agglomerate rock (Figs. A,F).

In culminating a long ecological succession, another redwood forest grew above the buried fossil forest. The new forest likewise was buried in volcanic ash and rock. It was petrified and its stratum hardened into agglomerate rock on the similar layer below it. Continuing in the Laramie (Upper Cretaceous) and Eocene periods, this whole long process of
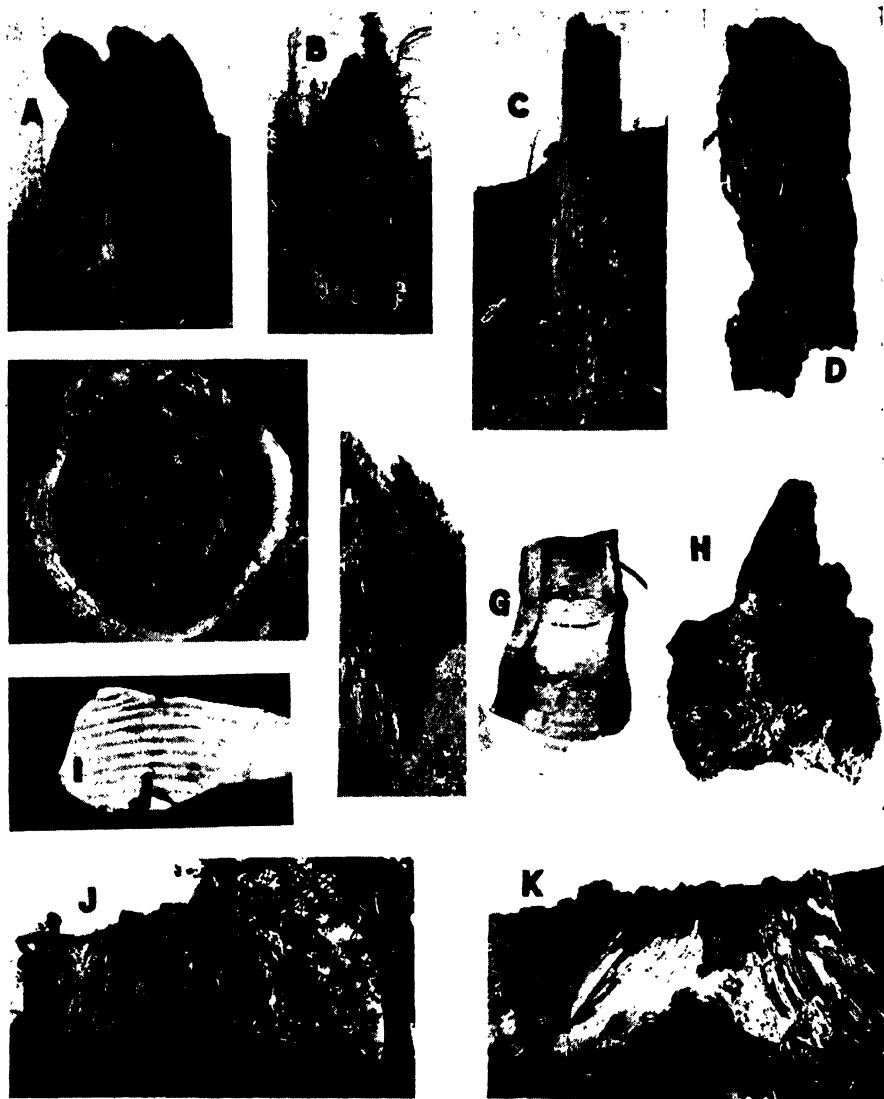
Figures A to K. All except figure I are·photographs of petrified wood of *Sequoia magnifica* found in the Gallatin Petrified Forests.

A. Pillar tree 20 ft. tall and 3 ft. in diameter, imbedded in cliff of agglomerate rock; found by writer in 1930. B. Trunk 13 ft. tall and 6 ft. in diameter. C. Trunk 15 ft. tall and 4 ft. in diameter. D. Piece of petrified wood containing many holes and grooves probably made by termites or wood boring beetles before the wood was petrified. ×⅕. E. Top of trunk 9 inches in diameter, inclosed by a cylinder of white quartz. F. Trunk 20 ft. tall and 3 ft. in diameter. G. Annual rings in piece of petrified wood. ×⅓. H. Wood that presumably was rotted by fungi before it was petrified. ×½. I. Petrified, yellow, elm-type wood of Oligocene period, found near Madison River. ×⅓. J. Stump 11 ft. in diameter. K. Stump 12 ft. in diameter, found at altitude of 10,000 ft.

ecological succession producing a redwood forest, volcanic rock burying the forest, subsidence of the land and petrification of the trees, and hardening of the stratum into agglomerate rock was repeated until at least 8 layers of fossil forests were buried in horizontal strata, as shown on one ridge (Fig. C).[4] Some of the strata were only a few feet thick and held only stumps and fallen logs, as only the parts of the wood in the agglomerate rock were preserved (Figs. J,K). Other strata were thick enough to hold vertical trunks 13 to 20 ft. tall as shown by the pillar tree with prominent roots and a top limited by the stratum of rock above it (Fig. A).

Some of the *S. magnifica* wood evidently was attacked by wood rotting fungi and boring insects before it was petrified, as effects like theirs were found in pieces of petrified wood (Figs. D,H).

When the Gallatin Mountain Range was raised, the strata bearing the petrified forests formed the upper part of some of the mountains. Erosion exposed parts of the fossil forests where they were found at altitudes of 7000 to 10,000 ft. at many places in an area nearly 40 miles long.

Petrified wood very different from the redwood was found on bluffs of the Madison River about 50 miles from the Gallatin Mountain Range. The specimens from the region of the Madison River presumably came from logs that floated on an Oligocene (Neocene) lake there. The logs were buried in sandy gravel in which they were petrified with silica. The largest log seen was 5 ft. long and 2 ft. in diameter. This petrified wood was white to light yellow and showed finely detailed structure of the tracheae and annual rings (Fig. 1). Recently broken surfaces were shiny on these fossils. This petrified wood probably is referable to a genus now occurring in low latitudes. Like the Gallatin Petrified Forests, the Madison River region merits further scientific study.

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TEXAS AGRICULTURAL EXPERIMENT STATION
JACKSONVILLE, TEXAS

Sex Organs of Angiopteris evecta

ARTHUR W. HAUPT

(WITH SIXTEEN FIGURES)

This paper is based on material kindly furnished by Professor W. J. G. Land, of the University of Chicago, who collected, in 1912, on the island of Tutuila, Samoa, many hundreds of gametophytes of *Angiopteris evecta* in various stages of development. A previous paper by Dr. Land (6), based on this collection, has dealt with certain phases of the embryogeny. In it he has fully described the conditions under which the gametophytes were found growing. Early accounts dealing with the gametophyte and sex organs of the Marattiaceae include those of Jonkman (5) on *Marattia* and *Angiopteris*, Farmer (4) on *Angiopteris*, Campbell (1) on *Marattia*, and Campbell (2) on *Kaulfussia*. In his comprehensive monograph of the eusporangiate ferns, Campbell (3) deals with all of the foregoing genera, as well as with *Danaea*. The present study confirms the account, given by earlier authors, of the development of the antheridium, and presents a description, in greater detail than has heretofore been given, of the development of the archegonium.

In the material studied, the largest prothallia were found to be approximately 10 mm. in diameter, but many were smaller. They are at first broadly cordate, becoming almost orbicular at maturity. Growth takes place by means of a group of initials situated at the base of the apical sinus. As in all of the other Marattiaceae, the median portion of the prothallium forms a thick cushion which projects below the ventral surface and gradually merges into the wings, these being but one layer of cells thick at the margins. An endophytic fungus is invariably present in the median portion, the mycelium being intracellular. Unicellular rhizoids arise from the ventral surface, especially from its median portion. The prothallia are monoecious, the antheridia appearing before the archegonia. The latter are borne in large numbers on the ventral side of the prothallium, where they are confined to the median cushion. The antheridia occur on both the upper and lower surfaces. Jonkman (5) found that some of the archegonia are dorsal in position, but Farmer (4) and Campbell (1) found that they are always ventral.

ANTHERIDIUM

The development of the antheridium resembles that characteristic of all of the eusporangiate ferns. A superficial initial gives rise, by a periclinal division, to an outer primary wall cell and an inner primary spermatogenous cell, the former dividing almost at once by an anticlinal wall, while the division of the latter may be either anticlinal or periclinal

(Figs. 1 and 2). With an increase in the number of spermatogenous cells by divisions in all three planes, the antheridium wall is completed by the cutting off of a layer of cells from the adjacent cells of the prothallium
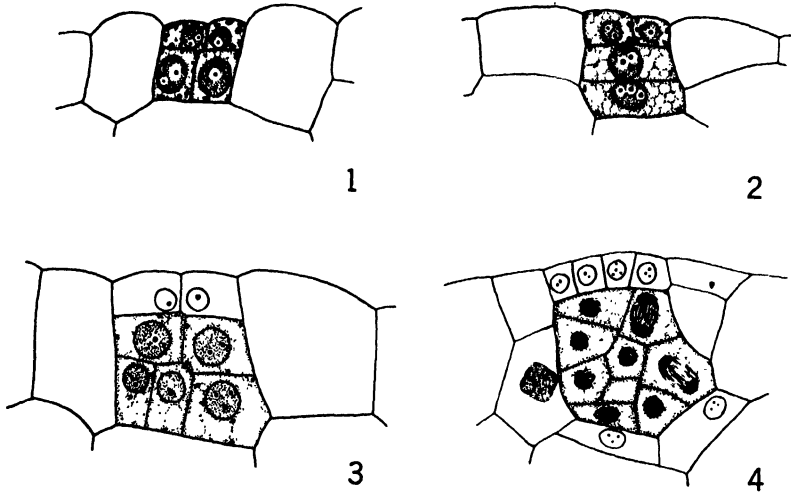
Figs. 1-4. Early stages in the development of the antheridium. ×300.

(Figs. 3 and 4). The later stages, which are well known, eventually result in the formation of a large number of coiled, multiciliate sperms.

ARCHEGONIUM

The superficial initial which gives rise to the archegonium produces, by a periclinal division, an outer primary neck cell and an inner cell (Fig. 5). The latter does not cut off a basal cell, but functions directly as the "central cell," producing the entire axial row. The primary neck cell, by means of two successive anticlinal divisions at right angles to each other, gives rise to four neck cells (Fig. 6). Then the central cell undergoes a periclinal division to form a ventral cell and a smaller neck canal cell (Figs. 7 and 8). The neck cells now increase in number, forming two tiers of four cells each (Fig. 9). Soon the ventral cell gives rise to the ventral canal cell and egg (Fig. 10). This occurrence is nearly always followed by division of the nucleus of the neck canal cell to form two nuclei that ordinarily are not separated by a wall (Figs. 11 and 12). Meanwhile the number of tiers of neck cells increases to three. The neck projects only slightly beyond the level of the surrounding cells of the prothallium. Soon after the protoplasts of the three cells belonging to the axial row begin to withdraw slightly from their walls, a sterile jacket
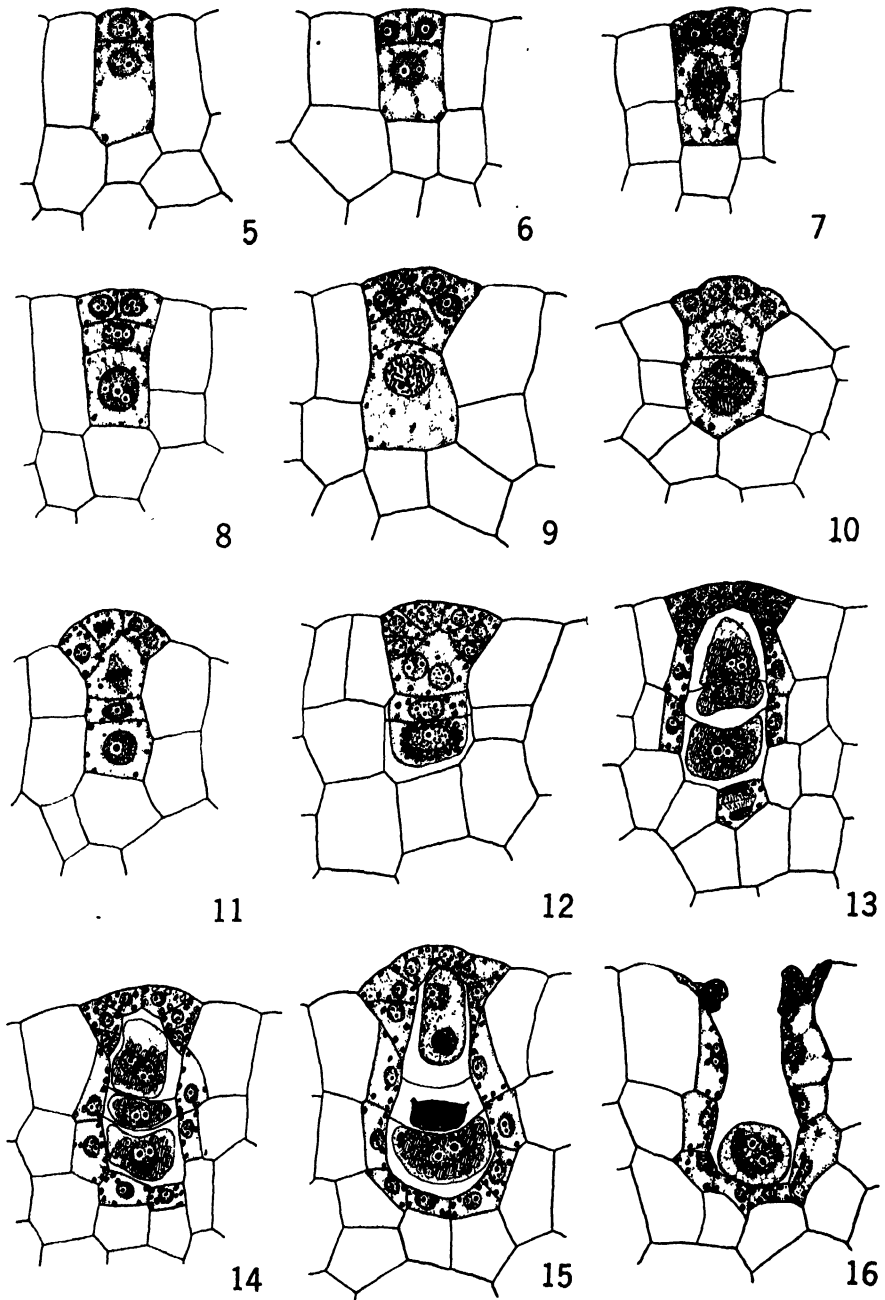
Figs. 5–16. Stages in the development of the archegonium. $\times 270$.

is cut off from the surrounding vegetative cells (Figs. 13–16). Typically the ventral canal cell is as large as is represented by the figures, but sometimes it is smaller.

Occasionally the nucleus of the neck canal cell fails to divide as early as has been described (Fig. 13), and possibly may not divide at all. Exceptionally its division is followed by the appearance of a transverse wall, which thereby forms two neck canal cells. Only one such case was observed. Jonkman (5) states that very often a transverse wall appears in the neck canal cell, dividing it into two cells. He figures an archegonium with two neck canal cells in both *Marattia* and *Angiopteris*. Apparently Jonkman did not observe an archegonium with a single binucleate neck canal cell. Farmer (4) reported that the archegonium of *Angiopteris* regularly has two neck canal cells; on the other hand, Campbell (1) found a single binucleate neck canal cell in *Marattia*.

The absence of a basal cell in the young archegonium was a constant feature of all of the material available for the present investigation. This is in agreement with the early observations of Jonkman (5). In *Angiopteris*, Farmer (4) found that a basal cell is usually absent, but he thought that it might be present in a few cases. In *Marattia*, Campbell (1) reported the occurrence of a basal cell, but in *Danaea*, he (3) found a basal cell to be constantly absent. In connection with the Marattiaceae in general, Campbell (3) states that a basal cell is usually, but not always formed. His figures show a basal cell in *Angiopteris* and *Kaulfussia*, but not in *Danaea*.

In its early developmental stages, the archegonium has small plastids which are more numerous than those in the surrounding cells of the prothallium. When the neck canal cell becomes binucleate, however, the plastids in the cells of the axial row increase in number and, by the formation of starch, in size as well (Figs. 13 and 14). The preparation of the egg for fertilization is accompanied by the breaking down of the ventral canal cell, neck canal cell, and neck cells. The egg, assuming a nearly spherical form, lies at the bottom of the archegonial cavity (Fig. 16). Although a great many archegonia are formed, only a few ripen, the rest degenerating. The mature archegonium shown in Fig. 16 is one of three of similar appearance found on the same prothallium.

As soon as fertilization has occurred and an embryo begins to develop inside an archegonium, all of the other archegonia degenerate and no new ones make their appearance. Land (6) says, "The massive archegonial pad bears numerous archegonia, but never more than one has been observed to function. Several thousand individuals were

examined, and never more than one embryo or sporeling was found on a prothallus." He states further that the necks of the functionless archegonia invariably fail[*] to open.

SUMMARY

The development of the antheridium is similar to that of the other Marattiaceae.

The archegonium develops without the formation of a basal cell.

The formation of the ventral canal cell and egg precedes the division of the nucleus of the neck canal cell.

With rare exceptions, a single binucleate neck canal is present.

Several archegonia may ripen at the same time, but fertilization results in the degeneration of all of the archegonia except the one fertilized.

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A further Study of Interglacial Peat from Washington

Henry P. Hansen and J. Hoover Mackin

(with two figures)

The Puget Lowland in Northwestern Washington has been subjected to at least two Pleistocene glaciations; the first of which is known as the Admiralty, followed by the Puyallup interglacial period, and the second as the Vashon (Bretz 1913). During the retreat of the Admiralty glacier, considerable ponding of water occurred, as is evidenced by the presence of silts, varved clays, and other types of lacustrine deposits. Peat lenses of varying magnitude are often present at different stratigraphic positions in the sequence of glaciolacustrine deposits. This paper is concerned with the pollen analysis of an interglacial peat stratum in Seattle, Washington (Hansen), and the position of the peat in the stratigraphic sequence in the Puget Lowland (Mackin). In a previous paper, Hansen (1938a) interpreted the forest succession during a brief interval of interglacial time from pollen analysis of a peat stratum located ten miles east of Auburn, Washington. That deposit is probably younger than that of this study, as will be discussed later. The post-Vashon forest succession and climate in the Puget Sound region, as interpreted from pollen analysis of bogs of post-Vashon origin, has also been worked out (Hansen 1938b). These interpretations may serve as criteria in the interpretations of the pollen spectra of this paper.

The peat of this study is located in Beacon Hill, in the south central part of Seattle. Extensive regrading for streets several years ago involved the removal of the Vashon till-mantle, exposing the interglacial sediments which form the core of the hill. The peat lenses crop out in a landslide scarp 210 to 220 feet above sea level, approximately 150 yards south of the Twelfth Avenue viaduct. The total thickness of the peat-bearing bed is about 64 inches. The lowest and thickest lens is about three feet thick; the lower half consisting of gray, silty, limnic peat, and grading upward into fibrous peat, which contains fragments of reed and sedge. This is followed upward by a series of thinner lenses of limnic peat, which contain some silt, and are interbedded by layers of silt and sand.

GEOLOGIC RELATIONS

General Statement

The Pleistocene stratigraphic sequence in the Puget Lowland, as recognized by Bretz (1913), includes from the base upwards: (1) Admiralty till, (2) Admiralty sediments, (3) Vashon till (Wisconsin age), and (4) post-Vashon glaciofluvial and glaciolacustrine deposits. In the

Seattle area the Admiralty sediments, generally flat-bedded, form the cores of a series of drumloidal hills, elongated in a north-south direction. The hills are enwrapped by a sheet of Vashon till, averaging 20 feet in thickness, but varying from 0 to 100 feet or more. Vashon retreatal sediments are highly variable in thickness and distribution; in general, they may be distinguished from the Admiralty sediments only by their stratigraphic relations to the Vashon till sheet. Bretz believes that the Admiralty sediments originally formed a proglacial aggradational plain in the central part of the Puget Lowland, with the surface of the approximate level of the present hill-tops; that this plain was trenched by north-south stream valleys during the Puyallup interglacial period, and that the valleys and divides were later modified into the present trough-drumloid topography by southward-moving Vashon ice.

Relations of Peat to Overlying Deposits

The relations of the Beacon Hill peats to the enclosing sediments are illustrated by the accompanying figure (Fig. 1). Although the Vashon till is not present in the immediate section, the peat is regarded as pre-Vashon because the overlying blue clays, silts, and gravels can be traced southward along the west flank of the Hill to a point where they are overlain uncom-
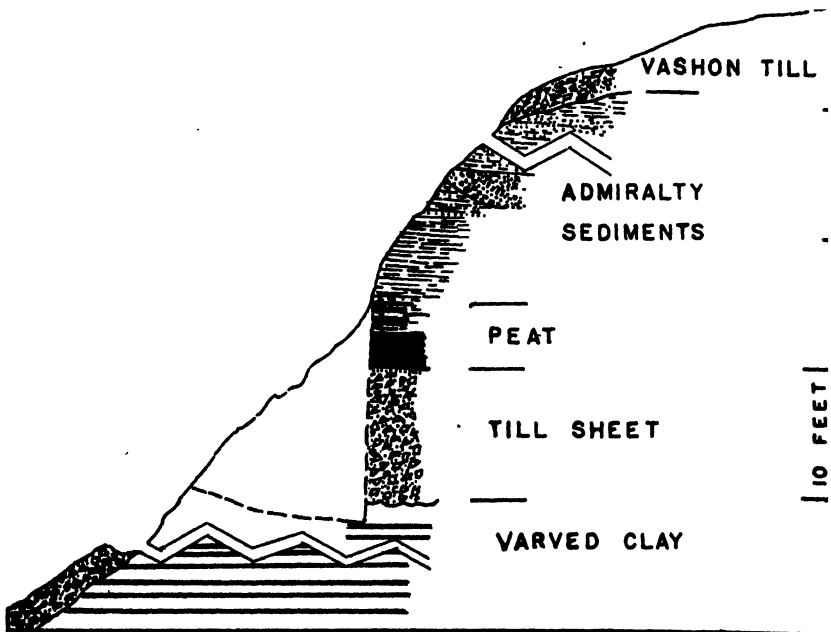
Fig. 1. Diagram showing relations of the Beacon Hill peat. Dashed line indicates outline of pit, excavated largely in rubble.

formably by Vashon till. Numerous cuts in the flanks and crests of adjacent hills show similar relationships. Bretz (1913) states that peat deposits were exhumed in the removal of Denny Hill, one and one-half miles to the northwest, where the relations of the peat layers to overlying Vashon till indicated that they were an integral part of the Admiralty sediments.

Relations of the Peat to Underlying Deposits

Landslide scarps in the lower flanks of the hill, below the level of the peat, show a 110 foot sequence of varved clays, recording approximately 500 years of sedimentation in a glacial lake. These clays are markedly different from the laminated to massive blue clays, with interbedded sand and gravel, which enclose the overlying peat beds. Individual varves are very thick at the base of the exposure, the annual units averaging 15 inches. The units thin progressively upward, averaging 1½ inches in the middle and upper parts of the sequence, but the top varves increase in thickness to a 2½ inch average. The uppermost several layers are 3 foot silt beds. Resting directly upon the silt is a 10 foot till sheet, containing striated pebbles in a gray silt matrix similar to the varve materials. The contact between the varve sequence and the till is sharp, with a 2 to 4 inch zone showing shearing and crumpling. The basal peat lens rests upon the till sheet, with a 6 inch layer of coarse sand at the contact.

The till sheet is not normally exposed at the present surface. The contact of varve, silt, till, and peat were seen in a 14 foot section, in a pit opened at a single place along the hill flank in the vicinity of the peat outcrops where topographic relations and the relative absence of land-slides were favorable for excavation. Since critical evidence is not now at hand, two alternative explanations of the relations of the peat to the underlying strata will be outlined briefly.

The first hypothesis holds that the complete Beacon Hill sequence is Admiralty in age, and is in harmony with the regional conclusions of Bretz, although he did not specifically recognize the existence of the varved clays in the Admiralty sediments. According to this view an initial retreat of Admiralty ice permitted the formation of a glacial lake in which varved sediments accumulated for approximately 500 years. Lacustrine sedimentation was brought to a close by readvance of the Admiralty glacier to the latitude of Seattle. Final retreat of the ice was followed by formation of peat, and the deposition of the thick sequence of blue clays, sands, and gravels, the typical Admiralty sediments of Bretz. This hypothesis is supported by the variation in varve thickness described above, since gradation from basal thick layers, to middle thin, to upper thick, suggests retreat followed by readvance.

A minor variation of the foregoing hypothesis attributes the cessation of varve sedimentation to the draining of the lake, the relatively great thickness of the upper varves to the turbidity of the shrinking waters, and the till to a stranded berg. This view finds some support in the thinness of the sheared zone at the base of the till and in the fact that the peat deposits are somewhat thicker over the till than in other parts of the bank, where excavations through the peat failed to discover till at a corresponding level. According to this view the peat accumulated in a kettle pond on the drained lake floor, approximately five hundred years after the Admiralty glacier had withdrawn from the Seattle area.

These hypotheses serve to explain all essential features of the Beacon Hill sequence, but one of the deduced consequences fails of confirmation. The varved clays must have been deposited in a relatively extensive water body, and, if they were formed as suggested above, should be present as a persistent lower member of the Admiralty deposits in adjacent areas. Excellent exposures in sea cliffs north and south of Seattle, however, show no varves, the typical Admiralty blue clays and sands extending from sea level to the hilltop mantle of Vashon till. It is recognized that lateral gradation or deformation might explain these circumstances, but in the absence of evidence favoring either possibility, a second hypothesis seems worthy of consideration.

This alternative hypothesis makes the Beacon Hill varves a part of a sequence of considerable lateral extent, formed in a proglacial lake during a pre-Admiralty glacial stage. The varved sequence then may have been maturely dissected by streams during a pre-Admiralty interglacial period, and the residual hills further eroded and blanketed by Admiralty till and the thick cover of Admiralty sediments. The composite sequence would then have been subjected to erosion by streams during the Puyallup interglacial stage, and finally covered with Vashon drift. This relatively complex history of repeated erosion and burial would explain the lack of continuous exposures of varved clays, particularly in view of the fact that all students of glaciation of the Puget Sound area are agreed that the base of the Admiralty till is generally below present tide level.

The final solution of these problems will require much detailed stratigraphic study, supplemented by pollen analysis, of the Pleistocene sequence in the Puget Lowland. For the purpose of the present paper it should be noted, that in spite of some uncertainties, the geological relations indicate that the peat stratum was deposited during an early stage in the Admiralty deglaciation of the Seattle area.

METHODS

Eleven peat samples were obtained at approximately six-inch intervals, although this varied somewhat depending upon the thickness of the inter-

bedded silt and sand which separated the upper peat lenses. A foot or more of the face of the exposure was removed in order to secure unweathered and unoxidized material. For study, the peat was pulverized in a mortar, boiled in a weak solution of potassium hydrate, washed, centrifuged, stained with gentian violet, and mounted in glycerin jelly. A total of 113 to 262 pollen grains were counted from each level. The number of pollen grains at each level is approximately indicative of their relative abundance (table 1).

TABLE 1
Percentages of Pollens at different depths

DEPTH IN INCHES	0	6	12	18	24	30	36	42	48	54	62
Pinus contorta	47	60	54	48	30	55	40	42	49	54	39
P. monticola	7	15	25	23	46	34	20	38	39	34	30
Picea sitchensis	0.5	3	1	1	3	7	33	5	5	6	22
Abies grandis	3	1	..	5	1	..	1	..	..	..	..
A. lasiocarpa	..	..	..	..	1	..	..	2	..	..	..
Tsuga	2	..	1	..	1	..	1	1	2	..	2
Gramineae	30	8	6	5	10	..	4	2	3	5	3
Compositae	3	0.5	0.5	1	2	1	..	3	1	..	1
Alnus	4	1.5	1	2.5	..	..	..	2	1	..	1
Acer	0.5	0.5	1	7	2	..	..	1	..	..	1
Betula	1	9	8	4	2	..	..	3	..	..	..
Salix	2	1.5	..	1.5	1	..	..	..	..	..	..
Chenopodiaceae	..	..	2	1.5	1	2	1	..	..	1	..
Cyperaceae*	..	6	2	31	19	23	50	37	4	22	24
Typha*	..	..	..	12	..	..	..	..	..	..	..
Sparganium*	..	..	..	1	..	..	..	..	..	..	..
Fern*	..	9	..	..	1	..	..	1	6	..	..
Unknown*	53	13	20	21	11	15	14	7	3	10	1
Total number	262	218	172	185	122	152	174	175	113	122	155

* Number, and not computed in the percentages.

It is realized that at best, pollen analysis and its interpretation is subject to many sources of error, which have been adequately discussed by various workers (Erdtmann 1931, Fuller 1935, Sears 1930). In the analysis of interglacial peat, however, the source of error attributed to age is greatly magnified. Obviously the degree of preservation of the pollens in the peat is one of the important factors in recording the correct representation of adjacent flora during the time the peat was being deposited. The older the peat the greater the chance for destruction of the less durable pollens, and distortion of the vegetative record. Thus it should be borne in mind that the pollen analysis of the peat of this study, and the interpretation of said analysis are discussed with full cognizance of its shortcomings.

SIGNIFICANCE AND CORRELATION OF THE POLLEN SPECTRA

The forests which existed in the Puget Lowland during the initiation of the peat accumulation, consisted chiefly of lodgepole pine (*Pinus contorta*) and western white pine (*P. monticola*), with an abundance of grass (fig. 2). The frequencies of these are 47, 7, and 30 per cent respectively in the lowest level. This forest, with other species in lesser abundance (table 1), may or may not have been the pioneer forests of the interglacial period. It would be hard to estimate the amount of time which had elapsed between the retreat of the Admiralty ice and the invasion by forests. The second hypothesis concerning the stratigraphic relations, however, indicates that at least 500 years had passed before the beginning of the peat deposition. The initial post-Vashon forests to invade the Puget Lowland, areas near Spokane, Washington, and in Northern Idaho, likewise consisted of lodgepole and white pines (Hansen 1938b, 1939a, 1939b). Each of these areas supports a different forest climax at present, although the initial post-Vashon forest succession was apparently similar. The presence of an abundance of grass in the early postglacial forest succession in Northern Idaho may indicate earlier tundra-like conditions, which had existed previous to forest invasion. Upon the basis of postglacial forest succession, it seems probable that the Seattle area was invaded by forests soon after the retreat of the Admiralty glacier. The percentage of grass pollens decreases from the lowest level to the top with slight fluctuations, and seems to offer no further significance.

Lodgepole pine increases to 60 per cent at 6 inches, and then decreases to 30 per cent at 24 inches. White pine shows a gradual increase from the lowest level, to 46 per cent at 24 inches to supersede lodgepole pine. This probably indicates normal forest succession, because lodgepole is less tolerant of shade than white pine, and is gradually replaced by the latter (Larsen 1930). Lodgepole pine again increases sharply at the next horizon, and then decreases at the 36 inch level. White pine decreases at both levels to record 20 per cent at 36 inches. Sitka spruce (*Picea sitchensis*) shows a sharp and significant increase to 33 per cent at the same level, which is its highest frequency throughout its spectrum. The present range of Sitka spruce indicates its preference for a very humid climate, as it reaches its maximum development in the fog belt area along the North Pacific Coast. Spruce records a sharp decrease to 5 per cent at the next higher level, and remains uniform to the uppermost level, where it again increases to 22 per cent. Lodgepole and white pines again show an increase from the 36 inch level; the first recording 54 per cent at 54 inches, and the latter 39 per cent at 48 inches. Both species decrease in frequency to the top level, with lodgepole recording 39 per cent and white pine 30 per cent. The presence of sedge pollens in all levels sampled
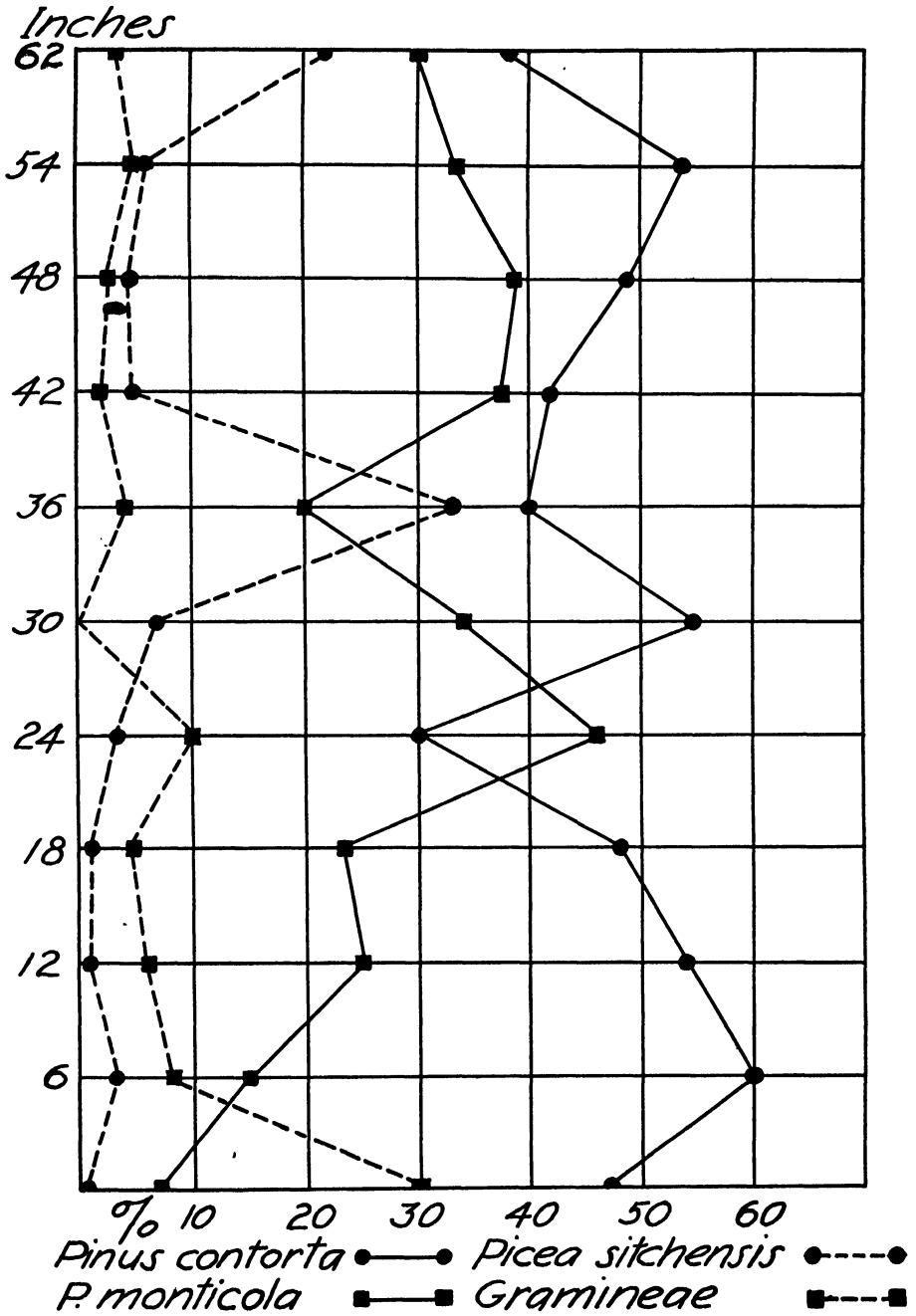
Fig. 2. Pollen diagram.

(table·1), and the absence of sphagnum moss leaves, with the exception of one at the 42 inch horizon, indicate that the bog existed in the sedge stage except when inundated. The greatest number of sedge pollen grains is recorded at 36 inches, the same level at which spruce reaches its maximum. Pollens of other species are present throughout, but not in sufficient numbers to be of importance in the indicated forest succession (table 1). Apparently lodgepole and white pines were dominant during the interval recorded by the peat deposit.

Hemlock, which shows a trace in most of the horizons, may be either western (*Tsuga heterophylla*) or mountain hemlock (*T. mertensiana*). Douglas fir (*Pseudotsuga mucronata*) which played an important part in the postglacial forest succession in the Puget Sound region, seems to be entirely lacking. The dearth of the pollens of these species may be of chronological significance as will be discussed later.

CHRONOLOGICAL CONSIDERATIONS

The period of time represented by the peat bearing strata is probably short, and represents a relatively small portion of the entire interglacial period. The fact that the peat is strongly compressed would indicate, however, that the time required for its deposition is longer than that for the same thickness of postglacial peat. Lesquereux (1885) estimates that peat in the lower levels of a deposit may be compressed to less than one-eighth of its original volume, but this would depend upon the thickness and composition of the peat. Estimates have been made for the time required for the accumulation of one foot of peat, with considerable differences of opinion by the various investigators (Sears 1933). These estimates range from 2 to 1665 years for peats in various parts of Europe and North America, accumulated under varying conditions. Sears estimates that about 300 years are required for the accumulation of a foot of peat in Ohio. The average depth of nineteen post-Vashon bogs in the Pacific Northwest, shown in a study of their profiles by Rigg (1938), is about 30 feet. This includes the lake mud and sedimentary (limnic) peat, which is taken into consideration here because it contains an abundance of pollen, records pioneer forest succession, and consequently may be used as a time factor. Upon the basis of the above figure, a foot of post-Vashon peat in this region required about 1000 years for its time of accumulation, because it is estimated by geologists that approximately 25,000 to 35,000 years have elapsed since the recession of the Vashon glacier. Considering the amount of compaction caused by its own weight, and that of the overlying sediments, as well as its great age, the peat of this study possibly required about 8000 years for its deposition. The total thickness of the peat itself is about 4 feet, and 2000 years per foot for its rate of accumulation does not seem an unreasonable figure.

As previously shown, the stratigraphic relationships of the peat stratum to the underlying till indicate that its deposition began soon after the retreat of the Admiralty ice from the Seattle area. That forests may exist in close proximity to a glacier is shown by the study of post-Middle Wisconsin forest succession in the driftless area of Wisconsin (Hansen 1939c), and the existence of intraglacial forests in eastern Wisconsin (Wilson 1932). The driftless area was apparently forested during the later stages of the Wisconsin glacial epoch, while forests also existed in eastern Wisconsin during the period of deglaciation between the retreat of the Middle and the advance of the Later Wisconsin ice sheets. Forests actually exist upon certain stagnated Alaska glaciers at present (Washburn 1935), while Cooper (1939), in extensive studies of plant succession in recently deglaciated valleys in Alaska, has shown that forests of spruce and hemlock follow closely in the wake of the receding ice. Climatic and edaphic conditions here may be somewhat similar to those which existed near the ice-front in the Puget Lowland during the Pleistocene. The absence of pollen in the underlying blue clays, silts, and varved clays may indicate the absence of forests until the beginning of the peat deposition.

The stage of forest succession reached at the time of deposition of the uppermost peat may also serve as a chronological criterion by comparison with post-Vashon forest succession. It should be mentioned, however, that forest succession is probably controlled largely by climate, and forest succession, as interpreted from pollen analysis, is one of the few evidences at hand by which one may reach conclusions with respect to interglacial and postglacial climatic fluctuation. As shown by the pollen record, the forests which existed at the beginning of the peat deposition, whether pioneer or later, consisted chiefly of two species which also were dominant in pioneer post-Vashon succession in the Pacific Northwest. As postglacial time in the Puget Sound region progressed, the pioneer species, lodgepole and white pines, were gradually replaced with Douglas fir and hemlock, with the former coming in first and more abundantly (Hansen 1938b). This occurred at a point approximately one-fourth from the bottom in each of two bogs. The time required for the deposition of the lower quarter of peat was perhaps almost one-half of postglacial time, because of the greater compression in the lower levels, and the presence of sedimentary peat, which requires more time for its deposition than a similar thickness of fibrous peat. If this assumption is correct, the replacement of the pioneer species by Douglas fir and hemlock did not occur until almost 15,000 years of post-Vashon time had elapsed. The absence of Douglas fir and the presence of only a trace of hemlock pollen in the peat concerned here indicate that either the climate had not moderated sufficiently for the advent of these species, or the time was too short to have allowed normal

forest succession to have reached that stage. In an interglacial peat stratum underlying the Auburn Delta, ten miles east of Auburn, Washington, both Douglas fir and hemlock pollen was present, as was also that of white fir (*Abies grandis*), white pine, lodgepole pine, and Sitka spruce. White fir and white pine were the dominant species throughout the section, which seems to represent a very brief interval in the upper level of the interglacial stratigraphic sequence (Hansen 1938a).

In a much thicker section of interglacial peats, clays, and silts near Everett, Washington, as high as 40 per cent of hemlock and 15 per cent of Douglas fir pollen was noted in a peat sample about half way up in the section. There is evidence that this section represents a considerable portion of interglacial time, and the presence of an abundance of hemlock and Douglas fir pollen indicates that the forest succession had reached a stage where these species played an important part. It also indicates that the climate was favorable for the existence of these species in the Puget Lowland during the latter half of interglacial time. Thus, the stratigraphic evidence for the peat being of early interglacial origin is further corroborated by pollen analysis, while the forest succession and the thickness of the peat stratum indicate that it represents a period of not over 8000 years duration.

CLIMATIC CONSIDERATIONS

In terms of climatic interpretation the presence of an abundance of grass, and lodgepole and white pine pollens in the lowest level, marks the existence of a cool and medium dry period during the earliest stage of peat deposition. This appears to have been similar to the early post-Vashon climate in the Puget Sound region, as interpreted from pollen analysis of post-Vashon bogs (Hansen 1938b). The sharp increase of spruce to 33 per cent at the 36 inch horizon apparently marks an increase in humidity and warmth. Its sharp decrease in the succeeding level indicates a recurrence of the earlier cool and medium dry climate, perhaps caused by a minor oscillation or readvance of the Admiralty glacier. A final period of greater humidity and warmth is perhaps reflected by an increase in spruce, and conversely, by a decrease in lodgepole and white pines. The dearth of Douglas fir and hemlock pollens throughout the section indicates that the climate had not moderated sufficiently at the time of termination of the peat deposition to be favorable for the invasion of these species.

SUMMARY

The geological and stratigraphical relationships of an interglacial peat deposit in Seattle, Washington, indicate that the peat was deposited during the early part of the Puyallup interglacial stage.

Pollen analysis of the peat tends to corroborate the geological evidence, because the initial forests of interglacial time consisted of species similar to those in the same area as well as in other regions in the Pacific Northwest during early post-Vashon time.

The thickness of the peat stratum and the stage of forest succession recorded in the uppermost level, indicate that the interval of time represented by the peat was only a small portion of the interglacial stage, and hypothetically did not extend over more than 8000 years.

In terms of climate, the forest succession suggests four poorly defined alternating periods of coolness and dryness, and warmth and humidity, beginning with the former.

It is fully realized that the age of the peat tends to increase the sources of error which are inherent in pollen statistics, and all conclusions drawn on the basis of pollen analysis may be taken for what they are worth.

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New Names and Transfers in the Lobelioideae

Rogers McVaugh

In the course of preparation of monographic studies on the *Campanulaceae*, subfamily *Lobelioideae*, it has been found necessary to make several new combinations and to provide specific names for some species which never have been properly characterized. A list of the new names follows:

1. **Diastatea micrantha** (H. B. K.) comb. nov. *Lobelia micrantha* H. B. K., Nov. Gen. & Sp. 3:316. 1819 (p. 247 of folio ed.). The genus *Diastatea* was described by Scheidweiler in 1841, and included a single species, *D. virgata*. The original description characterized the genus and species so well that the present writer has no hesitation in stating that *Diastatea virgata* is identical with *Lobelia ramosissima* Mart. & Gal., which was described in 1842. It is, indeed, possible that the plants grown by Scheidweiler at Brussels were from seeds collected by Galeotti in Mexico. Recent studies, soon to be published, indicate that there are six species in Mexico and Central America which form a good natural genus distinct from *Lobelia* and *Laurentia*. The earliest available generic name for these is apparently *Diastatea* Scheidw., Allg. Gartenz. 9: 396. Dec. 1841.

2. **Diastatea tenera** (A. Gray) comb. nov. *Palmerella tenera* A. Gray, Proc. Amer. Acad. 22:433. 1887. This species is certainly congeneric with the preceding and with *D. virgata*, and belongs neither with *Laurentia* nor to the artificial genus *Palmerella*, the type species of which is to be transferred to *Laurentia*, as indicated below.

3. **Heterotoma cordifolia** (Hook. & Arn.) comb. nov. *Lobelia cordifolia* Hook. & Arn., Bot. Beech. Voy. 301. 1840. This species has passed, for the most part, under the name of *H. tenella* Turcz. Bentham and Hooker recognized the identity of *Lobelia cordifolia* with *Heterotoma tenella*, but, following the so-called "Kew Rule" took up the first combination in the correct genus.

4. **Heterotoma flexuosa** (Presl) comb. nov. *Rapuntium flexuosum* Presl, Prodr. Mon. Lob. 23. 1836. *Lobelia arabidoides* Hook. & Arn., Bot. Beech. Voy. 301. 1840. The TYPE of *Rapuntium flexuosum*, collected in Mexico by Haenke (Herb. Mus. Nat. Pragae 495565) is clearly the plant which has been called *Heterotoma arabidoides*. Presl, oddly enough, failed to note the irregular, spurred calyx of this plant, although he recognized the character as being of generic importance and erected his genus *Myopsia* upon it. The identity of the single species of *Myopsia, M. mexicana,* is unknown, although it has usually been considered identical with *Heterotoma lobelioides* Zucc. There is nothing

in Presl's generic description to indicate which species of *Heterotoma* is meant, and Professor Ivan Klásterský states that the type is not to be located at Prague.

5. **Laurentia debilis** (A. Gray) comb. nov. *Palmerella debilis* A. Gray, Proc. Amer. Acad. 11: 80. 1876. The genus *Palmerella* is certainly an artificial one and not to be upheld. This has been recognized by Schönland and others, but the formal combinations under *Laurentia* have apparently never been made.

6. **Laurentia debilis** var. **serrata** (A. Gray) comb. nov. *Palmerella debilis* var. *serrata* A. Gray, Bot. Calif. 1: 619. 1876.

7. **Lobelia stenodonta** (Fern.) comb. nov. *Heterotoma stenodonta* Fern., Proc. Amer. Acad. 36: 504. 1901. A clearly marked species, allied to *Lobelia plebeia* E. Wimm. and to *L. longicaulis* Brandg. There is no indication of any relationship to *Heterotoma*.

8. **Lobelia robusta** Graham, var. **porto-ricensis** (A. DC.) comb. nov. *Tupa assurgens,* var. *porto-ricensis* A. DC., DC. Prodr. 7: 394. 1939. *Lobelia assurgens* L. is confined to Jamaica, with a well-marked variety in central and western Cuba. A similar but quite distinct species, *L. robusta,* is confined to Hispaniola and eastern Cuba, with the present variety known only from Porto Rico.

9. **Lobelia georgiana,** nom. nov. *Lobelia glandulifera* (A. Gray) Small, Fl. S. E. U. S. 1144. 1903, non *L. glandulifera* O. Ktze., Rev. Gen. Pl. 2: 378. 1891. Kuntze's name was a transfer of *Scaevola glandulifera* DC.

10. **Lobelia umbellifera,** nom. nov. *Lobelia fasciculata* Donn. Sm., Bot. Gaz. 27: 338. 1899, non *L. fasciculata* O. Ktze., Rev. Gen. Pl. 2: 378. 1891. Kuntze's name was a transfer of *Scaevola fasciculata* Benth.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION
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Additions to Florida Fungi—III

WILLIAM A. MURRILL

(WITH ONE FIGURE)

Numbers here cited refer to specimens in the herbarium of the Florida Agricultural Experiment Station, at Gainesville. My study of the Florida collections of *Marasmius* would have been practically impossible without the generous cooperation of Dr. F. J. Seaver, of the New York Botanical Garden.

Entoloma Westii sp. nov.

Pileo convexo, umbonato, 3 cm. lato, roseo-avellaneo; sporis angulatis, 10 × 6μ, stipite longo, glabro, albo, 6–8 × 0.2–0.3 cm.

Pileus convex to subexpanded with a sharp conic umbo 3 mm. high, gregarious, 3 cm. broad; surface smooth, glabrous, satiny, rosy-avellaneous, becoming hygrophanous, striate, and dull-vinose; margin projecting 2 mm., entire; context very thin, pallid; lamellae sinuate, broad, medium distant, inserted, entire, pallid to pink; spores angular, usually pentagonal, 1-guttulate, pink, about 10 × 6μ; cystidia none; stipe tapering upward, smooth, glabrous, shining, white, 6–8 × 0.2–0.3 cm.

Type collected by Erdman West on a much-decayed hardwood log in Sugarfoot Hammock, near Gainesville, Fla., Oct. 18, 1938 (*F 18274*). Wood-loving, with a long, slender stipe and a sharp, conic umbo. Very near *E. pinicola* Murrill but without the white incrustations and growing on hardwood instead of pine.

Russula cystidiosa sp. nov.

Pileo convexo-depresso, 5–7 cm. lato, miniato, striato, sapore grato; sporis spinulosis, ochroleucis, 8–12 × 6–10μ; cystidiis clavatis vel fusoideis, 30–60 × 8–12μ; stipite albo, 7 × 1–2 cm.

Pileus convex to depressed, gregarious, 5–7 cm. broad; surface somewhat viscid, glabrous, uniformly miniatous, peeling readily, margin entire, short-striate; context thin, white, unchanging, odorless, mild; lamellae attenuate behind, equal, not forked, medium broad and medium distant, entire, white to pale-yellow; spores subglobose to broadly ellipsoid, apiculate, spinulose, 1-guttulate, ochroleucous in mass, 8–12 × 6–10μ; cystidia clavate or fusoid, pointed or blunt, hyaline, thin-walled, about 30–60 × 8–12μ; stipe subequal, smooth, glabrous, white, unchanging when dried, about 7 × 1–2 cm.

Type collected by West, Arnold and Murrill under an oak in a high hammock at Sugarfoot, near Gainesville, Fla., Sep. 29, 1938 (*F 18353*).

Related to *R. subrubescens* but uniformly bright-red with milk-white stem.

Russula mutabilis sp. nov.

Pileo convexo-depresso, 5 cm. lato, viscido, luteo-brunneo ad rubro; sporis spinulosis, 7–8 × 6μ; stipite albo ad rubro, 4 × 1–1.3 cm.

Pileus convex to depressed, gregarious, about 5 cm. broad; surface distinctly viscid, smooth, glabrous, orange-brown, changing to dull-red within an hour after picking, purplish-black when dried; margin more or less striate, not peeling readily; context opaque, juicy, odor slightly like that of *R. foetens* when fresh, like varnish while drying, taste pungent, slightly astringent; lamellae adnate, rather broad, medium distant, forked at the base, entire, pallid or yellowish, reddish when dry; spores subglobose, densely and decidedly spinulose, hyaline under a microscope, 7–8 × 6μ; cystidia none; stipe tapering downward, smooth, glabrous, white, testaceous at the base, soon becoming blood-red below, purple-red when dried, 4 × 1–1.3 cm.

Type collected by West and Murrill on low ground under hardwood trees in Prairie Creek Hammock, southeast of Gainesville, Fla., July 27, 1938 (*F 17943*). When I first saw this plant I thought it was *R. foetens* and started to throw the specimens away, but a red tint on the cap restrained me. When I got to the herbarium the stems were as red as blood on the lower half, with no black. The caps also had deepened to dull-red and later became purplish-black. A determined effort to assign it to Beardslee's *R. rubescens* met with no success.

Russula subrubescens sp. nov.

Pileo convexo-depresso, 5 cm. lato, viscido, striato, roseo vel roseo-isabellino, sapore grato; sporis spinulosis, ochraceis, 9–11 × 7–8μ; cystidiis fusoideis, 60 × 10μ; stipite albo, 4–5 × 1–1.5 cm.

Pileus convex to deeply depressed, gregarious, 5 cm. broad; surface rather viscid, peeling readily, glabrous, short-striate, roseous, rosy-ochraceous or incarnate-isabelline; context thick, white, unchanging, odorless, mild; lamellae attenuate behind, not forked, equal, medium broad, crowded, entire, white to pale-yellow; spores subglobose to broadly ellipsoid, roughly and densely spinulose, ochroleucous or ochraceous in mass, 1–guttulate, 9–11 × 7–8μ; cystidia abundant, fusiform, pointed, smooth, hyaline, about 60 × 10μ; stipe equal or tapering downward, smooth, glabrous, white, sometimes ochraceous at the base, 4–5 × 1–1.5 cm.

Type collected by West, Arnold and Murrill on the ground under an oak in a high hammock at Sugarfoot, near Gainesville, Fla., Sep. 29, 1938 (*F 18339*). Also at the same time and place (*F 18349*). Suggesting *R. rubescens* Beards. but differing in color and gill structure.

Melanoleuca albissima floridana var. nov.

Pileo convexo-subexpanso,´ 6–12 cm. lato, albo, disco cremeo, praefelleo; lamellis albis, sporis globosis, 4μ; stipite albo, 4 × 0.6–1 cm.

Pileus convex to subexpanded, broadly umbonate at times, scattered to gregarious, 6–12 cm. broad; surface dry, smooth, glabrous, white, with cremeous disk, margin even, entire; context rather tough, drying readily, white, unchanging, with odor of anise, very bitter-farinaceous at once; lamellae adnexed or sinuate with long decurrent tooth, rather narrow, very close, inserted, some forked at the base, entire, white, unchanging; spores globose or nearly so, smooth, hyaline, about 4μ; cystidia none; stipe equal, smooth, glabrous, white, slightly pruinose at the apex, about 4 × 0.6–1 cm.

Type collected among leaves under hardwoods in Sugarfoot Hammock, near Gainesville, Fla., Oct. 18, 1938 (F 18287). Very near M. albissima (Peck) Murrill but with more crowded gills and smaller spores. The taste is not at all acrid and the spores appear to be entirely smooth. There is a great resemblance, however, to Peck's species as I remember it. Dried specimens are very light in weight.

Melanoleuca maculata sp. nov.

Pileo convexo-plano, 9 cm. lato, albo, maculato, felleo; lamellis albis, maculatis, sporis ovoideis, 5 × 3μ; stipite albo ad citrino, 6 × 1.2 cm.

Pileus convex to plane, gregarious, 9 cm. broad; surface smooth, glabrous, white with ferruginous spots and stains, margin incurved when young, even, entire, white, becoming lemon-yellow on drying; context white, unchanging, odorless, bitter, sweating profusely in drying; lamellae sinuate or adnexed, broad behind, much crowded, thin, fleshy, white, rusty-spotted, entire, drying slowly with exudation of much water; spores ovoid, smooth, hyaline, about 5 × 3μ; cystidia none; stipe equal, smooth, finely scurfy, becoming glabrous, milk-white changing to lemon-yellow on drying, 6 × 1.2 cm.

Type collected by W. A. Murrill on a much-decayed pine log at Sugarfoot, near Gainesville, Fla., Oct. 16, 1938 (F 18275). Suggesting Collybia maculata,but very juicy and partly changing to yellow in drying. The cap goes through a sweating process like a puffball, producing a dried specimen totally distinct from herbarium material of C. maculata; while the spores are ovoid instead of subglobose.

Melanoleuca Westiana sp. nov.

Pileo convexo-plano, 6.5 cm. lato, cremeo, piperato farinaceoque; sporis ellipsoideis, 5–7 × 3–4μ; stipite albo, 5.5 × 1.5 cm.

Pileus convex to plane, solitary, 6.5 cm. broad; surface smooth, glabrous, cremeous, margin deflexed, even, entire; context thick, firm, white, unchanging, acrid and farinaceous at once, with anise odor; lamellae sinuate, narrow, medium distant, inserted, undulate, pallid; spores ellipsoid, smooth, hyaline, 1–guttulate, 5–7 $\times$ 3–4μ; stipe tapering upward, smooth, pubescent, white, 5.5 $\times$ 1.5 cm.

Type collected by Erdman West on the ground under hardwood trees at Boulaware Springs, near Gainesville, Fla., July 17, 1938 (*F 17849*). Near *M. albissima* (Peck) Murrill but of different consistency and not drying white.

Prunulus marasmius sp. nov.

Pileo convexo-expanso, caespitoso, 1–1.5 cm. lato, griseo-albo; lamellis adnatis, albis, sporis ellipsoideis, 4.5 $\times$ 3μ; stipite glabro, albo ferrugineoque, 6 $\times$ 0.1–0.2 cm.

Pileus convex to expanded, slightly umbilicate at times, densely cespitose, about 1–1.5 cm. broad; surface dry, smooth, glabrous, grayish-white, margin even, entire to rimose; context very thin, white, odorless, slightly astringent; lamellae adnate, narrow, distant, inserted, white to discolored, entire; spores ellipsoid, smooth, hyaline, 1–guttulate, about 4.5 $\times$ 3μ; stipe equal, smooth, glabrous, white above, ferruginous below, about 6 $\times$ 0.1–0.2 cm.

Type collected by West, Arnold and Murrill on a much-decayed hardwood log in Kelley's Hammock, ten miles northwest of Gainesville, Fla., July 21, 1938 (*F 18277*). Also collected by the same persons at Grove Park, Fla., July 15, 1938 (*F 18270*). Very thin and partially reviving but having the general appearance of *Mycena*.

Marasmius caesius sp. nov.

Pileo convexo, 5–8 mm. lato, pulverulento, caesio vel albo; lamellis adnatis, albis, distantibus; sporis ellipsoideis, 4 $\times$ 3μ; stipite pruinoso, albo et murino vel atro, 1–1.5 $\times$ 0.1–0.2 cm.

Pileus convex, gregarious, 5–8 mm. broad; surface smooth, pulverulent or finely tomentose, caesious or whitish, fading with age; context membranous, pallid, odorless; lamellae adnate, distant, rather broad, inserted, entire, white, unchanging; spores broadly ellipsoid, smooth, 4 $\times$ 3μ; spore-print a mass of stellate, nodulose or irregular bodies 6μ and more in diameter, some resembling jack-rocks; stipe tapering downward, pruinose, white above, murinous to black-ish below, 1–1.5 $\times$ 0.1–0.2 cm.

Type collected by W. A. Murrill on fallen oak sticks in a high hammock at Gainesville, Fla., May 28, 1938 (*F 18263*). Also collected by West and Murrill on trash under oaks at the Tung-oil Mill, west of

Gainesville, June 22, 1938 (*F 18358*); and on sticks in oak woods at Gainesville in November, 1932 (*F 9927, F 9935*). The blue color fades quickly and does not appear in dried specimens.

Marasmius floridanus sp. nov.

Pileo convexo-subexpanso, gregario, 2–3 cm. lato, fulvo; lamellis adnatis, subdistantibus, albis; sporis 6–8 $\times$ 2.5–3μ; stipite glabro, albo vel fulvo, 3–7 $\times$ 0.2–0.4 cm.

Pileus convex to subexpanded, gregarious, 2–3 cm. broad; surface smooth, glabrous, fulvous; context submembranous, odorless, mild, white; lamellae adnate, inserted, rather narrow, subdistant, entire, white; spores narrowly pip-shaped, smooth, hyaline, 6–8 $\times$ 2.5–3μ; stipe equal, smooth, glabrous, shining, white or fulvous, 3–7 $\times$ 0.2–0.4 cm.

Type collected by West, Arnold and Murrill on a decayed hardwood log in Planera Hammock, July 16, 1938 (*F 17347*). Also collected several other times on dead wood in hammocks near Gainesville during the summer of 1938 (*F 17719, F 17731, F 17754, F 16388, F 17431*). Very striking and handsome and remaining attractive when dried. Suggesting *M. Berteroi* (Lév.) Murrill, of tropical America, but with much closer gills.

Marasmius heliomyces sp. nov.

Pileo convexo, 3–4 cm. lato, rugoso, subbadio ad cinereo; lamellis latis, distantibus, albis; stipite glabro, 5–6 $\times$ 0.3–0.5 cm.

Pileus hemispheric to broadly convex, not expanding, gregarious or solitary, 3–4 cm. broad; surface glabrous, much wrinkled radially and furrowed, pale-bay when fresh, becoming grayish on drying; margin entire to undulate or rimose; context membranous, white, unchanging, odorless, mild; lamellae sinuate, broad, triangular, distant, inserted, entire, white, unchanging; microscopic examination not satisfactory; stipe equal, hollow, smooth, glabrous, shining, white to bay, about 5–6 $\times$ 0.3–0.5 cm.

Type collected by West and Murrill on dead hardwood in Planera Hammock, eleven miles northwest of Gainesville, Fla., Aug. 2, 1938 (*F 18269*). Also collected by E. West on the base of an oak stump at Gainesville, Nov. 1, 1932 (*F 9931*). A rare species suggesting *Heliomyces* and related to *M. Berteroi* (Lév.) Murrill, of tropical America.

Marasmius nolaneiformis sp. nov.

Pileo convexo-plano, 1.5 cm. lato, striato, umbrino, fibrilloso; sporis ovoideis, 7–8 $\times$ 4–5μ, stipite umbrino, 3 $\times$ 0.1 cm.

Pileus convex to plane with small umbo, gregarious, about 1.5 cm. broad; surface hygrophanous, zonate, avellaneous and striate on the broad margin, umbrinous over the center and avellaneous on the disk, finely fibrillose-squamulose over the entire surface; context membranous, pallid, odorless, taste nutty; lamellae adnexed, broad, rounded behind, inserted, distant, entire, rosy-isabelline; spores ovoid, smooth, hyaline, granular, 7–8 × 4–5μ; cystidia none; stipe equal, solid, slightly enlarged at the base, pale-umbrinous or isabelline, finely scurfy, about 3 × 0.1 cm.

Type collected by W. A. Murrill in an open lawn at Gainesville, Fla., May 31, 1938 (*F 18259*). Suggesting *Nolanea* but the spore-print is chalk-white.

Marasmius setulosus sp. nov.

Pileo convexo, umbonato, 1–2 cm. lato, fulvo, hispidulo; lamellis fulvis, spinuliferis, sporis 10–12 × 4–4.5μ; stipite albido badioque, hispidulo, 3–4 × 0.15–0.2 cm.

Pileus convex with broad umbo, gregarious, 1–2 cm. broad; surface smooth, finely hispid, fulvous, darker on the umbo, margin even, entire; context subfleshy, thin, white, odorless, mild to slightly astringent; lamellae adnexed, rounded behind, medium broad, medium distant, inserted, entire, fulvous, unchanging; spores pip-shaped, smooth, hyaline, 1–guttulate, 10–12 × 4–4.5μ; cystidia abundant, pointed, ventricose, hyaline, 45–75 × 5–8μ; stipe equal, smooth, finely hispid, pallid above, bay below, 3–4 × 0.15–0.2 cm.

Type collected by West and Murrill in trash under an oak at Arredonda, Fla., July 29, 1938 (*F 18267*). Also collected by West and Murrill under hardwood trees at Kelley's Hammock, ten miles northwest of Gainesville, Fla., Aug. 3, 1938 (*F 18271*). Suggesting *M. glabellus* Peck but densely covered with fine, straight, sharp, hyaline bristles, while the gills also bristle with long, pointed cystidia. One of the most bristly fungi I ever met.

Marasmius sicciformis sp. nov.

Pileo conico, 1 cm. lato, sulcato, vinoso; lamellis adnatis, albis; sporis 8 × 5μ, cystidiis 80μ; stipite vinoso, glabro, 3 × 0.1 cm.

Pileus conic, solitary, 1 cm. broad; surface striate-suleate, glabrous, pale-vinose, darker on the umbo, margin entire; context membranous; lamellae adnate, inserted, broad, medium distant, white, entire; spores broadly ellipsoid, smooth, hyaline, about 8 × 5μ; cystidia few, pointed, tapering from a rather thick base, smooth, hyaline, projecting about 80μ; stipe equal, smooth, glabrous, shining, subconcolorous, hollow, 3 cm. long and less than 1 mm. thick.

Type collected by W. A. Murrill on the ground, probably attached to buried wood, at Gainesville, Fla., April 8, 1938 (*F 16179*). A rare species, beautiful in shape and color, with long, pointed cystidia.

Marasmius squamosidiscus sp. nov.

Pileo convexo, caespitoso, 3–5 cm. lato, albo, disco ferrugineo-squamuloso; lamellis adnatis, sporis ellipsoideis, 4–5 × 3–3.5μ; stipite squamuloso, albo, 3–4 × 0.3 cm.

Pileus convex, cespitose, 3–5 cm. broad; surface white, the disk decorated with ferruginous scales; margin even, entire to undulate; context subfleshy, thin, white, odorless, sweet and nutty; lamellae adnate, narrow, crowded, inserted, entire, white, unchanging; spores copious, ellipsoid, smooth, hyaline, 4–5 × 3–3.5μ; stipe equal, squamulose, white, unchanging, about 3–4 × 0.3 cm.

Type collected by West, Arnold and Murrill on a much-decayed hardwood log in dry oak-pine woods at Grove Park, Fla., July 15, 1938 (*F 18262*). Suggesting *Collybia maculata* in miniature in coloration but cespitose and scaly.

Marasmius subarchyropus sp. nov.

Pileo convexo-plano 4–6 cm. lato, pallido; lamellis albis, sporis ellipsoideis, 5–6 × 3–4μ; stipite pallido, pruinoso, 6–9 × 0.4–0.8 cm.

Pileus convex to plane or depressed, gregarious, 4–6 cm. broad; surface smooth, glabrous, pallid, pale-yellowish when dry; context subfleshy, white, odorless; lamellae adnexed, or adnate with a decurrent tooth, very crowded, very narrow, inserted, entire, white; spores ellipsoid, smooth, hyaline, 5–6 × 3–4μ; cystidia none; stipe equal, ridged at the apex, pallid, pruinose to sub-glabrous, 6–9 × 0.4–0.8 cm.

Type collected by West and Murrill on much-decayed hardwood in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 20, 1938 (*F 18264*). Resembling *M. archyropus* (Pers.) Fries but much larger and with different spores.

Marasmius subgraminis sp. nov. Fig. 1

Pileo convexo-expanso, 4–8 mm. lato, albo; lamellis adnatis, distantibus; sporis 7–9 × 3–4μ; stipite glabro, pallido, 5–10 × 0.5–1 mm.

Pileus membranous, convex to very slightly depressed, neither umbonate nor umbilicate, densely gregarious to cespitose, 4–8 mm. broad; surface dry, glabrous, not shining, white or slightly stramineous, margin undulate, sometimes rimose, slightly sulcate with age, deflexed on drying; context very thin, white, odor agreeable, taste slightly astringent; lamellae squarely adnate,

Fig. 1. Marasmius subgraminis Murrill. ×2.—*Photo by G. F. Weber.*

without a collar, plane, rather broad, distant, slightly interveined, several times inserted, entire on the edges, pallid to isabelline; spores pip-shaped, smooth, hyaline, not consistently guttulate, about 7–9 × 3–4μ; stipe lumpy, usually much enlarged and finely striate at the apex, white above and slightly rosy-avellaneous below, glabrous, 5–10 × 0.5–1 mm.

Type collected by Dr. George F. Weber on dead centipede grass on his lawn in Gainesville, Fla., Oct. 5, 1938 (F *18361*). Related to *M. graminis* Murrill, which was discovered on dead Bermuda grass on lawns in Cuba. The spores were found and studied by Dr. Weber after fruitless efforts on my part. The photograph reproduced herewith was taken by him.

Marasmius subnigricans sp. nov.

Pileo convexo, gregario, 1.5–3 cm. lato, albo, subnigricante; lamellis adnatis, distantibus, albis, subnigricantis; sporis 8–10 × 3–4μ, cystidiis 30 × 10–15μ, stipite albo, 3–4 × 0.2–0.3 cm.

Pileus campanulate to broadly convex, often umbonate, gregarious, 1.5–3 cm. broad; surface smooth or rugose, glabrous, pure-white, usually becoming partly or wholly blackish on drying; margin entire to undulate, even or sul-cate-striate; context membranous, white, changing to blackish, odorless, mild;

lamellae squarely adnate, narrow, distant, inserted, interveined, entire, white, becoming blackish; spores narrowly pip-shaped, smooth, hyaline, 8–10 × 3–4μ; cystidia abundant, bottle-shaped, usually abruptly pointed, hyaline, projecting about 30 × 10–15μ; stipe equal, smooth, glabrous, white, unchanging or darkening slightly when dried, about 3–4 × 0.2–0.3 cm.

Type collected by W. A. Murrill on hardwood sticks in a high hammock at Gainesville, Fla., July 1, 1938 (*F 17358*). Very common about Gainesville on fallen hardwood sticks, especially on oak (*F 17359, F 16324, F 9925, F 9937, F 9938*). Rather surprising in its change from pure-white to almost black. *M. nigripes* (Schw.) Fries is described as having angular spores and a black, horny stem.

Marasmius subprasiosmus sp. nov.

Pileo convexo, gregario, 2–3 cm. lato, sulcato, cremeo, alliaceo; sporis 5 × 2.5μ, stipite albo, pruinoso, 3–4 × 0.2 cm.

Pileus convex to subexpanded, slightly umbilicate at times, gregarious to subcespitose, 2–3 cm. broad; surface glabrous, radiate-sulcate, cremeous with a fulvous tint, the disk pale-fulvous; context tough, membranous, odor slight but distinctly alliaceous, taste mucilaginous and alliaceous; lamellae adnexed, narrow, unequal, distant, entire, white; spores subfusiform, smooth, hyaline, about 5 × 2.5μ; cystidia none; stipe enlarged below, smooth, pruinose, white, about 3–4 × 0.2 cm.

Type collected by W. A. Murrill on a lawn in Gainesville, Fla., May 31, 1938 (*F 18362*). Strongly suggestive of *M. prasiosmus* Fries in some of its characters.

Marasmius substenophyllus sp. nov.

Pileo convexo-subexpanso, 1.5–2.5 cm. lato, albo, glabro; lamellis decurrentibus, albis, sporis ellipsoideis, 6 × 4μ; cystidiis clavatis, 20–45 × 6–8μ; stipite albo, glabro, 1.5–3 × 0.2–0.3 cm.

Pileus convex to subexpanded, gregarious, 1.5–2.5 cm. broad; surface dry, smooth, white, glabrous, margin even, entire; context subfleshy, thin, white, odorless, slightly bitter; lamellae decurrent, inserted, distant, rather narrow, entire, white; spores copious, ellipsoid, smooth, hyaline, 1–guttulate, about 6 × 4μ; cystidia abundant, smooth, hyaline, usually clavate, projecting 20–45 × 6–8μ; stipe subequal, smooth, white, glabrous, with a white disk at the base, about 1.5–3 × 0.2–0.3 cm.

Type collected by West, Arnold and Murrill on dead hardwood in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 21, 1938 (*F 18268*). Also collected by West and Murrill in Sanchez Ham-

mock, July 23, 1938 (*F 18272, F 18276*). Reminding one of the common tropical species, *M. stenophyllus*, but thicker, more fleshy, and white throughout.

Marasmius subsynodicus sp. nov.

Pileo membranaceo, convexo-plano, gregario, 5–7 mm. lato, pallido; lamellis adnatis, distantibus, albis; sporis ovoideis, 4–5 × 2μ; stipite albo vel pallido, 5–10 × 0.5 mm.

Pileus membranous, convex to plane or slightly depressed, gregarious to subcespitose, 5–7 mm. broad; surface smooth, finely pulverulent under a lens, pale-isabelline to white, margin entire, even; context very thin, white, mild, odorless; lamellae adnate with a slight decurrent tooth, broad, distant, inserted, white, stramineous when dry, entire; spores few, oblong-ovoid, smooth, hyaline, about 4–5 × 2μ; stipe equal, smooth, finely fibrillose, white above, pallid with a rosy tint below, 5–10 × 0.5 mm.

Type collected by W. A. Murrill on chips and sticks in a pine grove at Gainesville, Fla., Oct. 21, 1932 (*F 9932*). Also collected by Dr. G. F. Weber on dead grass on a lawn in Gainesville, Oct. 2, 1938 (*F 18356*). Related to *M. synodicus* (Kunze) Fries. It is a small white species, densely gregarious and plentiful.

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made:

> *Melanoleuca maculata* = **Tricholoma maculatum**
> *Melanoleuca Westii* = **Tricholoma Westiana**
> *Prunulus marasmius* = **Mycena marasmius**

HERBARIUM FLORIDA AGRICULTURAL EXPERIMENT STATION
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Development of the Embryo-sac of Gagea fascicularis Salisb.

A. C. JOSHI

(WITH 11 FIGURES)

The development of the embryo-sac of *Gagea fascicularis* Salisb. (*G. lutea* Ker-Gawl.) was studied by Stenar (1927), and he described it to correspond to the *Lilium*-type, now called the *Adoxa*-type, with the modification that one of the chalazal nuclei of the 4-nucleate embryo-sac did not undergo the third division and the mature embryo-sac therefore possessed only two antipodals. The recent investigations of *Gagea ova*, *G. graminifolia* and *G. tenera* by Romanov (1936) and *G. minima* by Westergård (1936), on the other hand, have shown that the development of the embryo-sac in all these species corresponds to the *Fritillaria*-type. The development of the embryo-sac of *Gagea fascicularis*, therefore, needs reinvestigation.

The material used in the investigation was collected by me from Khilanmarg in the Kashmir State. Plants of *Gagea fascicularis* grow here at a height of 8000 to 13,000 feet. They flower mostly during the month of May, but a few flowers could still be seen at higher elevations about the 20th of June, 1938, when I visited this locality, and these were collected. They were fixed in Navashin's fluid and studied according to the customary methods. A few stages were found to be missing in this material, but fortunately these are sketched by Stenar (1927), and by considering them along with the stages present in my own preparations it has been possible to complete the series.

OBSERVATIONS

The ovary is trilocular and there are two rows of ovules in each loculus except in the upper portion. Here the ovules form only one row. They are anatropous and bitegmic. The outer integument is three cells thick, while the inner is mostly two cells thick except in the micropylar region, where it is' thicker. The micropyle is formed only by the inner integument. The nucellus is poorly developed (Fig. 1). About two rows of central cells in the chalazal region of the nucellus have denser cytoplasm than the rest. These connect the chalazal end of the embryo-sac with the vascular bundle of the ovule which ends in the chalaza and probably help in the transmission of food materials from the vascular bundle to the embryo-sac.

The archesporium is hypodermal and is mostly limited to one cell (Fig. 1). Stenar (1927) observed two or three archesporial cells in exceptional cases, but I did not come across any such in the present material. No parietal cell is cut off and the primary archesporial cell directly becomes the megaspore-mother cells.

The megaspore-mother cell stage is of very long duration. The ovules remain at this stage till the flowers open and the anthers dehisce. After this the development of the embryo-sac is very rapid and all stages from the megaspore-mother cell to the mature embryo-sac may be seen in the same ovary. As the material was collected from a far off place, it has not been possible to determine if further development of the embryo-sac from the megaspore-mother cell stage is conditioned by previous pollination. It is however quite possible that such a relation may exist and the embryosac may begin to develop in the ovules only after the flower has been pollinated. It is well known that in the Orchidaceae ovules do not develop until pollination of the flower occurs. *Gagea fascicularis* shows a comparatively primitive stage from which this highly specialized behavior of the Orchidaceae could have evolved.

The first division of the nucleus of the megaspore-mother cell, which is the reduction division, is not followed by any wall formation and results in the development of a 2-nucleate embryo-sac (Figs. 2–4). The next division leads to the development of the 4-nucleate embryo-sac. During this division as the daughter nuclei reach the telophase stage, the homotypic spindles become connected by secondary spindle fibres (Figs. 5 and 6). These spindle fibres are a new development as described by Stenar (1927) and not the remnants of the heterotypic spindle as believed by Schaffner (1897) and Coulter and Chamberlain (1903) from their studies of *Lilium*, because no such spindle fibres are seen at the 2-nucleate embryo-sac stage (Fig. 4). The nuclei in the 4-nucleate embryo-sac are at first nearly uniformly distributed (Fig. 6). Later the spindle fibres between the two micropylar nuclei disappear, while the other two spindles contract. The result is that one nucleus is left at the micropylar end of the embryo-sac and the remaining three are drawn toward the chalazal end (Figs. 7 and 8). During the next division of the nuclei the three chalazal nuclei fuse and a new 4-nucleate embryo-sac arises with two small nuclei at the micropylar end and two large nuclei at the chalazal end (Fig. 9). The number of nucleoli shows that the chalazal nuclei are triploid. One more division of the nuclei occurs to complete the development of the embryo-sac (Fig. 10), but during this division one of the
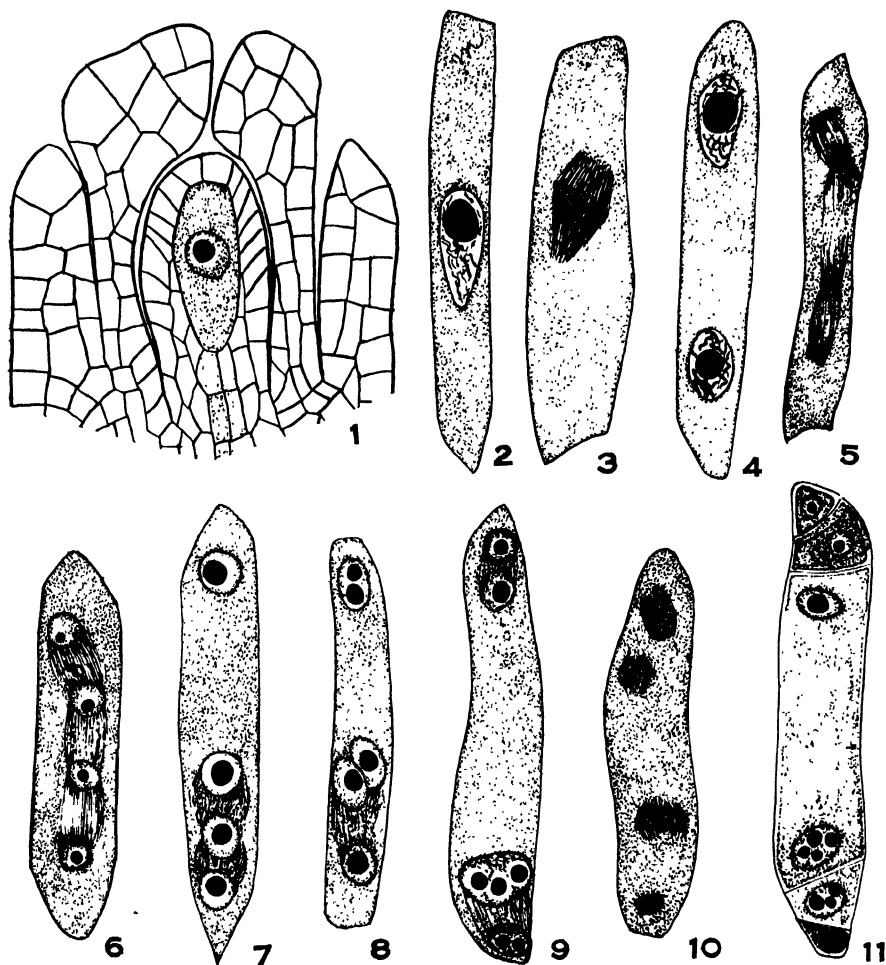
Gagea fascicularis Salisb.

Fig. 1. Part of a longitudinal section of an ovule at an early megaspore-mother cell stage showing the structure of the integuments and the nucellus.

Figs. 2–3. Megaspore-mother cell, heterotypic division, prophase and metaphase.

Fig. 4. 2-nucleate embryo-sac.

Figs. 5–6. Two stages in the development of the 4-nucleate embryo-sac.

Figs. 7–8. 4-nucleate embryo-sacs showing 1 + 3 arrangement of the megaspore nuclei.

Fig. 9. A secondary 4-nucleate embryo-sac.

Fig. 10. The fourth nuclear division in the development of the embryo-sac.

Fig. 11. 7-nucleate embryo-sac.

Figs. 2, 5 and 10 after Stenar (1927), the rest original. Fig. 1, ×300; Figs. 2–11, ×700.

chalazal nuclei fails to divide. It begins to degenerate. The embryo-sac is thus ultimately only 7-nucleate (Fig. 11). There is a normal egg-

apparatus, a haploid micropylar polar nucleus and triploid chalazal polar nucleus and two antipodals, out of which the chalazal antipodal is in a degenerating condition from the very beginning of its differentiation.

It is thus clear that in *Gagea fascicularis* in the development of the 7-nucleate embryo-sac from the megaspore-mother cell four nuclear divisions occur. The megaspore nuclei show 1+3 arrangement. During the third nuclear division the three chalazal nuclei fuse giving rise to a secondary 4-nucleate stage with larger triploid chalazal nuclei, as Bambacioni (1928) has shown in *Fritillaria persica* and Cooper (1935) in *Lilium Henryi*. The development of the embryo-sac, therefore, corresponds to the *Fritillaria-type*, as in species of *Gagea* investigated by Romanov (1936) and Westergård (1936).

SUMMARY

The ovules remain at the megaspore-mother cell stage until the anthesis of the flowers. No parietal cell is cut off. The primary archesporial cell directly develops into the megaspore-mother cell and later into the embryo-sac. The development of the embryo-sac corresponds to the *Fritillaria*-type with the modification that one of the chalazal nuclei after the second 4-nucleate stage does not divide and the complete embryo-sac is only 7-nucleate and 6-celled.

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Inflorescence, Floral anatomy and Morphology of Leitneria floridana *

ERNST C. ABBE AND T. T. EARLE

(WITH 37 FIGURES)

INTRODUCTION

This study of the perennially puzzling family, the *Leitneriaceae*, was undertaken with two related objectives in mind. The more important of these was felt to be an evaluation on an anatomical basis of the morphology of the much reducěd flower and inflorescence. The desirability of a re-examination of the family from this point of view was suggested by the better understanding of the floral and inflorescence morphology of other amentiferous families which has. followed a careful examination of their vascular anatomy (Fisher, 1928; Abbe, 1935, 1938). The second objective was to circumscriBe somewhat, the colorful wanderings of the family in the various phylogenetic "systems." Until much more is known about the Angiosperms this latter objective must remain largely the expression of a pious hope, nevertheless it seems to the writers that certain broad lines of relationship suggest themselves upon a re-evaluation of the available èvidence.

A few wořds of general information concerning the family may well be introduced at this point. The family consists of the single species, *Leitneria floridana* Chapm., which occurs in isolated fresh- or brackish-water swamps and sloughs in parts of Florida, Georgia, Arkansas, Missouri, and Texas (Sargent, 1926). The plant is a shrub or small tree up to twenty feet in height, with pale, fissured bark and with thick and firm leaves, which are bright green above and below are pale and coated with

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a villous pubescence. The wood is soft and exceedingly light, the character to which the plant owes its common name of "Cork Wood."

The writers are indebted to the late Professor Duncan S. Johnson, of Johns Hopkins University, who kindly collected the staminate and pistillate inflorescences used in this investigation. The trees which were the source of the material grow on the Johns Hopkins University campus. The fixing fluid was a chrom-acetic mixture. The material was subsequently stored in 70 per cent alcohol. Prior to detailed investigation the inflorescences were transferred to distilled water and permitted to soak for some time, which facilitated dissection. Representative dissections were drawn to scale and then were run up through the usual N-butyl alcohol series. Serial sections, 9 micra in thickness, were made and were stained with crystal violet and erythrosin in all series except one, which was stained with safranin and fast green. Camera lucida drawings of the sections were made and from these the three-dimensional figures were reconstructed to scale.
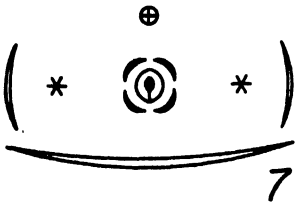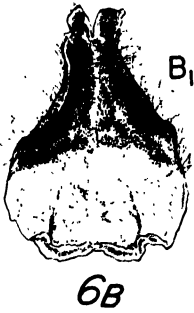
PISTILLATE FLORETS AND INFLORESCENCES

External Morphology.—At the time of pollination the pistillate flowers are sessile and solitary in the axils of the relatively large, spirally arranged primary bracts, each floret being flanked by two smaller secondary bracts. The primary axis of the inflorescence is stiffly erect. Owing to the combination of large overlapping bracts and small flowers the term ament would be completely applicable to the pistillate inflorescence if it were not for this stiff primary axis. The whole inflorescence may therefore be considered a "spike-like" ament. After pollination there is a recognizable lengthening of the secondary axes too slight to justify a change in the designation of the inflorescence. While most of the primary bracts of the inflorescence have pistillate flowers in their axils, the last two or three at the apex, and a still larger number at the base have no flowers in their axils.

Explanation of Figures 1–8

Figs. 1–8. Habit sketches and floral diagrams of pistillate flowers and cymules of *Leitneria floridana.* Figs. 1–3. Adaxial (dorsal), lateral, and abaxial (ventral) views, respectively, of a pistillate cymule from the upper part of a spike. Fig. 4. Floral diagram of following figure. Fig. 5. Dorsal view of axil of primary bract (B_1); pistil removed; secondary bracts (B_2), tepals, and region of attachment of pistil visible. Fig. 6A–6E. Dissected pistillate cymule. 6A. Secondary bract; 6B. Primary bract; 6C. Secondary bract; 6D and 6E. Young pistil with tepals, showing the short pedicel of the flower. Fig. 7. Floral diagram of the following figure. Fig. 8. Pistillate cymule (the pistil "lifted out").

All figures to the same scale. Note scale between Figs. 7 and 8.

1

2

3

4

B_1 B_2

tepal

primary axis

5

B_2

B_1

B_2

6A

6B

6C

tepals

tepals

6D

6E

B_2

tepals

B_1

8

1 mm

7
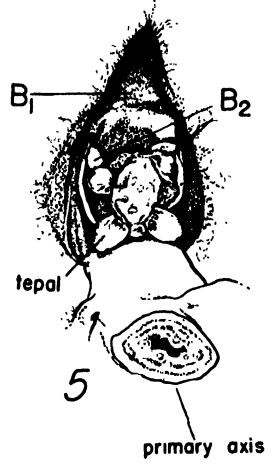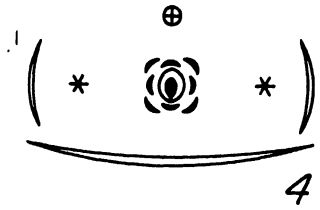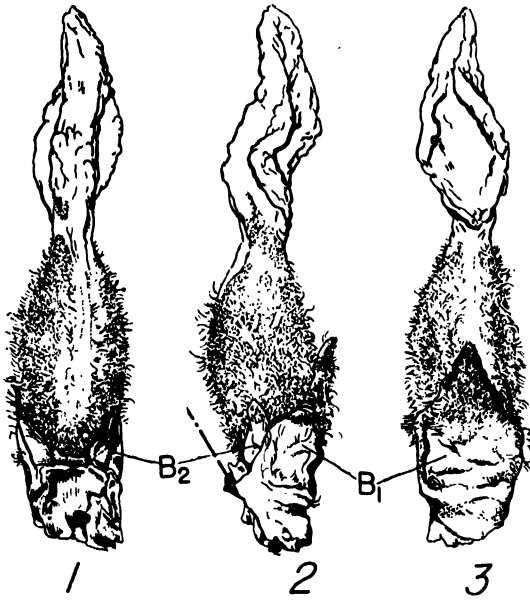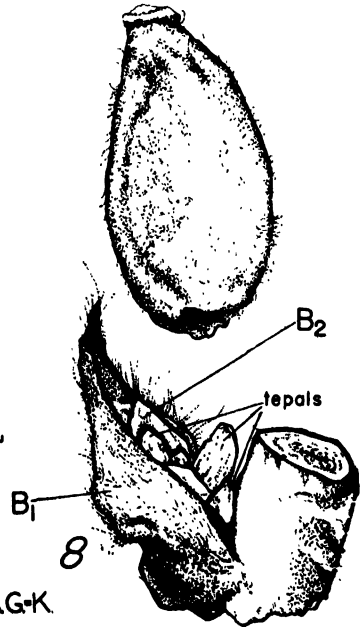
L.A.von.G.K.

The individual pistillate floret (figs. 1–3, 6D–E, 8) consists of a simple pistil surrounded at the base by very small tepals (figs. 5, 8). The placenta is on the abaxial side of the pistil, and bears a single anatropous ovule, which is attached toward the upper end of the placenta. The ovary is narrowly ovate in form, and is covered with dense short, crisp pubescence, which is practically absent in a narrow median longitudinal line on both the adaxial (fig. 1) and the abaxial (fig. 3) sides of the ovary. The ovary is crowned with a prominent fleshy stigma (figs. 1–3), which is lost by abscission at the base soon after fertilization (fig. 8).

Surrounding the base of the ovary is a perigon composed of diminutive tepals varying in number from three to about eight (figs. 4–5). The usual complement is four (figs. 6E, 7), in the diagonal radii. The tepals are inserted at the end of an extremely short pedicel, or secondary axis. Attached to this secondary axis there are consistently, in our material, two opposite secondary bracts (B_2, figs. 1, 2, 5, 6A, 6C, 8).

The writers found no evidence of vestigial stamens in the forty or fifty pistillate flowers which they examined. Further observations, however, might substantiate Baillon's (1880) report of bisexual florets.

Vascular Anatomy.—The primary axis of the pistillate inflorescence has a vascular cylinder broken up by the elongate combined leaf and branch gaps which results in a marked dictyostelic condition (fig. 22). From the base of each gap there arises the primary bract bundle (B_1) which passes through the cortex of the primary axis (fig. 22 level A), and of the secondary axis. Soon after the primary bract becomes free from the axis of the ament (fig. 22, level C) the primary bract bundle breaks up abruptly into a number of minor branches, which anastomose with each other (fig. 6B). Occasionally a minor anastomosis may connect the primary bract bundle with the vascular system of the secondary axis, or there may be some branching and recombining on the way out to the primary bract (fig. 22, between levels A and B), but this does not obscure its course. Whether the anastomoses are an indication of the suppression of the lateral bundles is not clear.

From either side of the combined leaf and branch gap in the primary axis there departs a branch trace. The two branch traces, one or the other of which may split (fig. 22, level A) and recombine almost immediately in the cortex of the primary axis, broaden somewhat to form two arcs (in transverse section, between levels A and B) as they pass into the secondary axis. These arcs are separated by abaxial and adaxial gaps which fail to close until after the lateral departure of the secondary bract bundles (B_2). The vascular system of the secondary axis thus becomes four-parted immediately after the departure of the secondary bract bundles.

These four bundles of the secondary axis form a dictyostele which becomes the vascular cylinder of the pedicel of the solitary floret (level B). The bundles, after a short distance, as a result of the closing of the gaps, form a loose cylinder of vascular tissue. This promptly breaks up again to form five bundles (fig. 22, between levels B and C), the abaxial ones very quickly uniting to form the compound ventral bundle (*vn*, level C) of the simple pistil. The adaxial bundle becomes the dorsal bundle (*dr*, level C) of the pistil, and continues unbroken (except for minor anastomoses) throughout the length of the pistil to form one of the three bundles of the stigma (level E). The two remaining bundles (level C) at the base of the ovary are so frequently associated with the dorsal in their origin that their interpretation as branches of the dorsal seems justifiable, although they sometimes become distinct at the same level as do the dorsal and ventrals.

A relatively infrequent occurrence, noted in only two cases, was the development abaxially in the median plane of a definite, but short-lived diminutive bundle (fig. 22, *ves* 3, between levels B and C) from a gap, whose sides ultimately continue on to form the ventrals of the pistil. This bundle (*ves* 3) the writers are inclined to interpret as a vestige of the vascular supply to a second carpel, although this must remain as an inference only, since there is no external evidence of a second carpel in the material studied. Vestigial 3 could also be interpreted as a continuation of the vascular tissue of the floral axis.

Almost immediately after the union of the two ventrals to form the fusion ventral (*vn*, fig. 22, just above level B), one or both of the branches of the dorsal splits (fig. 22, just above level C), one-half anastomosing with the fusion ventral, and the other half forming a lateral branch *y*. From the place of union of half of the branch of the dorsal with the fusion ventral there arises a small bundle *x*. The bundles *x* and *y* then branch repeatedly throughout the wall of the ovary, anastomosing with each other, and with the fusion ventral and dorsal to form the network of bundles characteristic of the fruit of *Leitneria*. The greater part of this anastomosing network is omitted from the reconstruction since it obscures the more important features.

This pattern of branching of the vascular tissue is quite remarkable, and has been well illustrated (Heim, 1892; Sargent, 1895 and 1926; Trelease, 1895). It resembles the similar, but less extensive, anastomosing vascular tissue which occurs in the ovary walls of mature fruits of the magnoliaceous genus, *Illicium*.

Except for the minor anastomoses which develop between the fusion ventral and the vascular network of the ovary wall, there are but few changes in the course of the fusion ventral to the stigma. Sometimes a

small branch develops (fig. 22, *ves* 2) which continues adaxially for a short distance in the median plane from near the base of the fusion ventral. This may well be a vestigial ovule bundle, although no evidence was noted of the occurrence of any such ovule in our material. As the fusion ventral continues toward the upper end of the ovary it broadens slightly. When it is approximately opposite the upper limit of the loculus it divides into three branches. The two lateral bundles, which evidently represent the original ventrals, continue on into the stigma, forming two of its three bundles. The bundle between the two ventrals bends abruptly downward and for a short distance travels in the wall of the ovary parallel to the fusion ventral. At the funiculus, the bundle gently bends adaxially and continues downward into the ovule. Soon after it enters the ovule it splits into three major branches, the outer branches of which continue unbroken to the chalaza of the ovule. The central bundle frays out into four or five smaller bundles which also terminate at the base of the ovule. No evidence was found of vascular bundles elsewhere in the ovule at this stage of development (shortly after fertilization). In one case, just above the funiculus, the ovule bundle developed a branch (fig. 22, *ves* 1) which ran for a short distance downward into the ovary wall between the fusion ventral and the ovule bundle. Its significance is not clear, although in our opinion it could well be interpreted as an aborted ovule bundle, since a second ovule might be expected to arise from the other margin of the carpel.

Mention should be made of the sporadic occurrence of isolated vascular bundles in the tepals. In several florets xylem composed of but one or two tracheids was observed towards the distal end of one or two of the tepals. In no case was there a connection of these traces with the vascular system of the pedicel. A similar case of an isolated bundle was noted in one of the smaller secondary bracts.

STAMINATE FLORETS AND INFLORESCENCES

External Morphology.—The staminate inflorescence consists of 40–50 cymules situated in the axils of large, spirally arranged, primary bracts.

Explanation of Figures 9–21

Figs. 9–21. Figs. 9, 10. Reduced staminate cymule from terminal portion of inflorescence. Fig. 11. Floral diagram of cymule shown in preceding figures. Figs. 12, 13. Dorsal and lateral views of staminate cymule from central portion of inflorescence. Fig. 14. Floral diagram of preceding figures. Fig. 15. Floral diagram of following figure. Fig. 16. Dorsal view of staminate cymule from central portion of inflorescence. Figs. 17, 19. Dorsal and lateral views, respectively, of staminate cymule from lower portion of inflorescence. Fig. 18. Floral diagram of cymule shown in figures 17 and 19. Fig. 20. Dorsal view of staminate cymule from lower portion of inflorescence. Fig. 21. Floral diagram of preceding figure. All figures to the same scale as in Figs. 1–8.

primary axis

primary axis

primary axis

primary axis

primary axis

primary axis

1 mm

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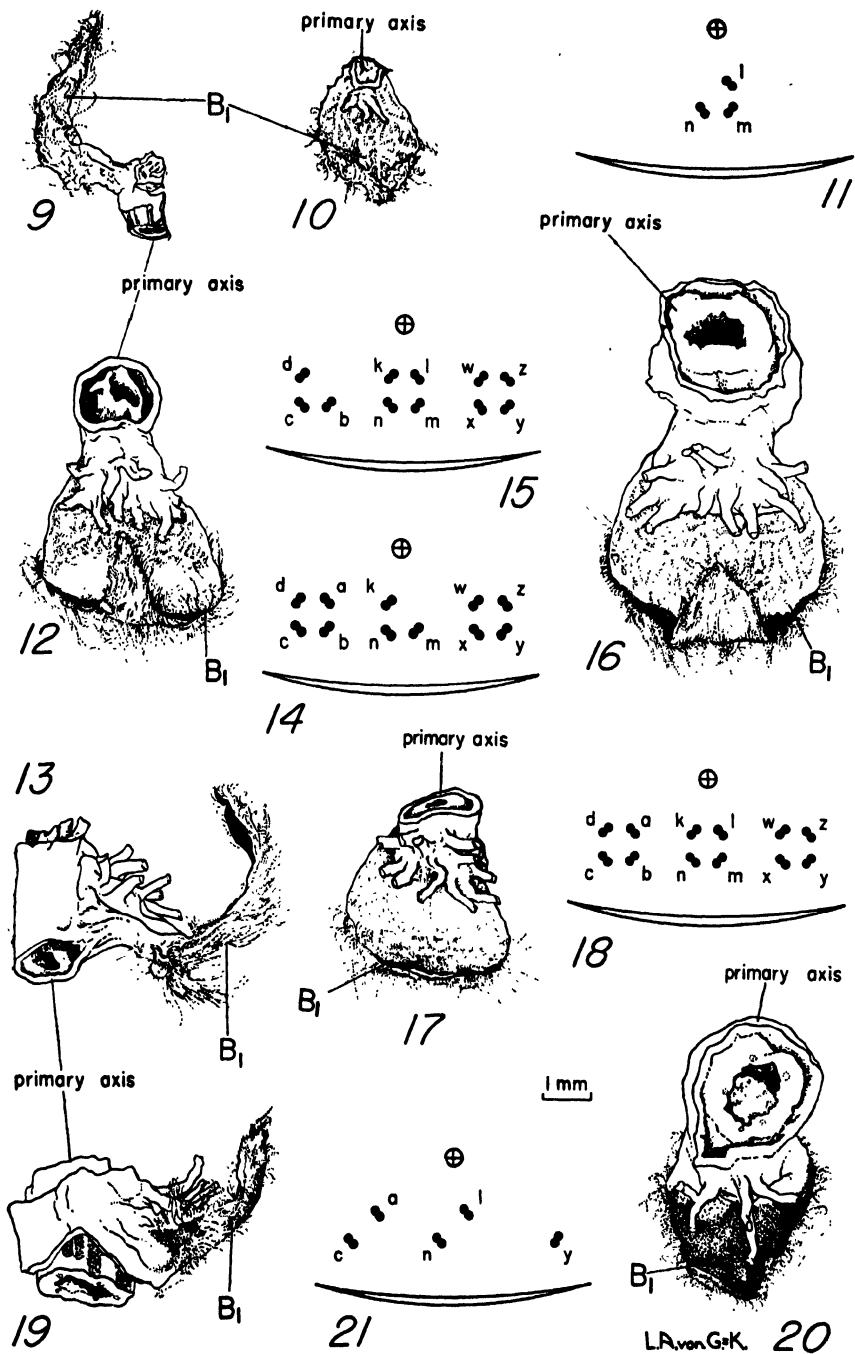
Secondary bracts are absent. Unlike the pistillate inflorescence, the primary axis of the staminate inflorescence is lax, characteristic of a true ament. The bracts are covered on their abaxial surface with a dense growth of glandular pubescence. Van Tieghem and LeComte (1886) have reported as many as 15 stamens in the axils of the bracts but in our material the cymules contain from 3 to 12 stamens each. The number of stamens largely depends on the location of the cymule in the ament, being least toward the basal and apical regions. At the extreme base and apex the primary bracts are entirely devoid of stamens. Baillon (1880) has reported the presence of small, unequal bracts surrounding the stamens, sometimes united to form a small perianth, but no evidence of these structures has been found in our material, either externally or in the distributional pattern of its vascular tissue.   .

The cymules in the central part of the ament usually consist of 10–12 stamens, arranged in three groups (figs. 12, 16, 17). The justification of assigning the stamens to three groups on the basis of external morphology will be seen when the vascular anatomy of the staminate cymule is described. It is sometimes difficult to place a particular stamen in a particular floret, because of the crowding of the three florets in the cymule, but the position is usually made clear when the internal anatomy is examined, as will be shown subsequently. Even in the apical (figs. 9, 10) and basal (figs. 19, 20) cymules, which consist of a greatly reduced number of stamens, the allocation of the various stamens to particular florets is facilitated by an examination of the vascular anatomy of the cymule.

Vascular Anatomy.—The vascular cylinder of the primary axis is broken by the many leaf and branch gaps into a dictyostele (fig. 24). The cymules in the lower region of the ament show the least modification in their vascular anatomy. Figure 26 is a reconstruction of the vascular system of a cymule from the lower part of an ament. The trace to the primary bract (B_1) passes out from the primary axis and is unbranched in the bract until it is beyond the region where the branch bundles terminate

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Explanation of Figures 22–29

Figs. 22–29. Reconstructions of the vascular systems of pistillate and staminate florets and cymules. Fig. 22. A composite three-dimensional reconstruction of a pistillate floret and cymule, from the central portion of the spike. Fig. 23. Floral diagram of the cymule shown in preceding figure. Fig. 24. Three-dimensional reconstruction of staminate cymule from central part of an ament (cf. Fig. 16). Fig. 25. Floral diagram of cymule shown in preceding figure. Fig. 26. Three-dimensional reconstruction of staminate cymule from lower part of an ament (cf. Fig. 17). Fig. 27. Floral diagram of preceding figure. Fig. 28. Floral diagram of following figure. Fig. 29. Three-dimensional reconstruction of greatly modified staminate cymule from terminal portion of ament (cf. Figs. 9 and 10).

The scale of each reconstruction is shown by a line equivalent in length to 1 mm. near each figure.
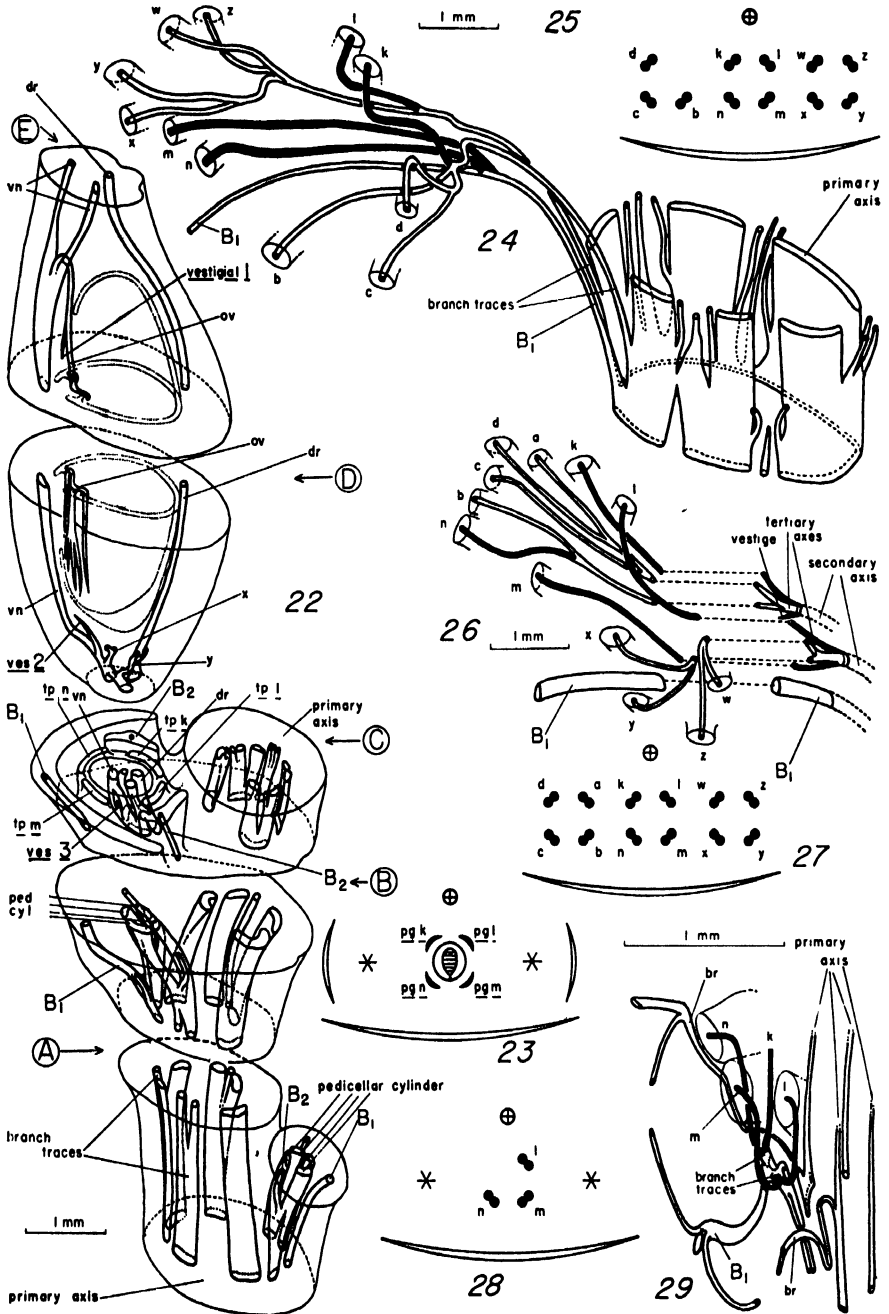
in the stamens, and it then breaks up into smaller bundles (cf. fig. 16).

Arising from each side of the gap are the two branch traces, which pass out in a gentle curve toward the group of stamens representing the cymule. These two arcs of vascular tissue represent the vascular system of the secondary axis. As soon as these arcs arrive in the base of the primary bract each forms a large central branch, flanked by two small branches. The small branches continue in an abaxial direction while the large central branches diverge abruptly to supply the lateral groups of stamens. Topographically, these large branches represent the vascular supplies to the tertiary axes, which, in the absence of secondary bracts, fill the gap at their origin. A short distance out from their origin they branch more or less dichotomously to supply the four stamens of each of the lateral florets.

The small bundles which arise on either side of the supply to the tertiary axes represent the continuation of the secondary axis and continue more or less in the median region, ultimately supplying the stamens of the secondary floret. In the cymule illustrated (fig. 26) the bundle labelled *vestige* continues for but a short distance and fails to supply a stamen. The stamen n, whose position suggests that it belongs to the secondary floret, receives its vascular supply as a branch from the trace to one of the stamens (b) of a tertiary floret. If stamen n is a member of the secondary floret, its vascular supply has anastomosed with that of the tertiary florets, an occurrence which is not without precedent in concentrated inflorescences of this type. That its origin should remain as a stub is somewhat unexpected, however. An alternative explanation would be to attribute a pentamerous state to one of the tertiary florets, and a trimerous one to the secondary floret, also not inconceivable, although not in keeping with our observations of the cymules in our material. We are inclined to adopt the former explanation, but with the reservation that the evidence is not conclusive.

The vascular system of a characteristic cymule from the central portion of an ament is shown in figure 24. This differs from the staminate cymule already described in the specific modifications which are associated with the vascular supply to the secondary floret. Two of the stamens, m and n, receive their supplies as branches from the primary bract bundle (B_1), a result of the transfer by fusion of the stamen bundles to the primary bract bundle. This is not an isolated instance as is shown by an analogous occurrence in the staminate cymules of *Corylus* (Abbe, 1935), in which the more modified cymules show this same relationship between the supply to the secondary floret and the primary bract trace. To return to *Leitneria*, the other two stamens, k and l, of the secondary floret have a less modified relationship to the remainder of the vascular system, in that they

merely depart rather tardily from the supply to the tertiary florets. With the less modified condition shown in figure 26 as an intermediate, there can hardly be any question that the average or more usual condition shown in figure 24 is but slightly modified and represents a triflorous cymule.

Of interest in indicating the effect of extreme crowding is the reduction in the staminate cymule of *Leitneria* shown in figures 9 and 10. Associated with this reduction is a marked modification of the vascular system of the cymule (fig. 29). The cymule is from the terminal portion of an ament. The two bracts above this had no flowers in their axils. The basic plan of the vascular system of the *Leitneria* cymule is much modified, embodying the complete loss of a vascular supply to the tertiary axes. Not only the vascular supplies to stamens m and n (as in fig. 24), but also the supplies to k and l, are derived by branching from the B_1 bundle. Fortunately there is a precedent already established in a less condensed portion of the inflorescence which permits the interpretation of two of these bundles as supplying stamens of the secondary floret. That the other two bundles may belong to this secondary floret is a logical conclusion, which is strengthened by the unusual supplementary vascular supply (*br*) to the primary bract. These two bundles (*br* and *br*) arise from the sides of the gap and topographically should be branch bundles, but their destination as part of the vascular system of the primary bract suggests that they have been modified from their original function. With the transference of the vascular supply of the median floral elements to the major median vascular bundle (B_1), the persistence of the branch bundles (*br* and *br*) is much to be wondered at and is apparently one of the vagaries to which the vascular system of the plant is subject. While these might be interpreted as corresponding to lateral bundles of the typical trilacunar supply of the foliage leaf (Sinnott, 1914), or even as secondary bract bundles, such contentions could hardly be maintained because the condition occurs in the most reduced part of the ament, while it is absent in less reduced regions.

SUMMARY OF INFLORESCENCE AND FLORAL MORPHOLOGY

The pistillate inflorescence.—This has its vascular system (fig. 34) but slightly modified from a normal condition (fig. 36). The primary bract bundle (B_1, fig. 34) is a clear-cut entity, as are the branch traces. The branch traces form a slightly dissected secondary axis cylinder from which secondary bract bundles (B_2) depart in the typical fashion.

The pistillate flower.—After the departure of the secondary bract bundles the four vascular bundles remaining (pedicellar cylinder, fig. 34) reorganize in the pedicel of the solitary pistillate flower to form the elements of the vascular supply to the simple pistil. There is some evi-

dence (vestige, fig. 34) to suggest that there may have been a second carpel in the gynoecium. Although the number of tepals varies, vascular tissue occurs in them but rarely, and even then there is no connection of this tissue with the main vascular system. Within the pistil there is evi-
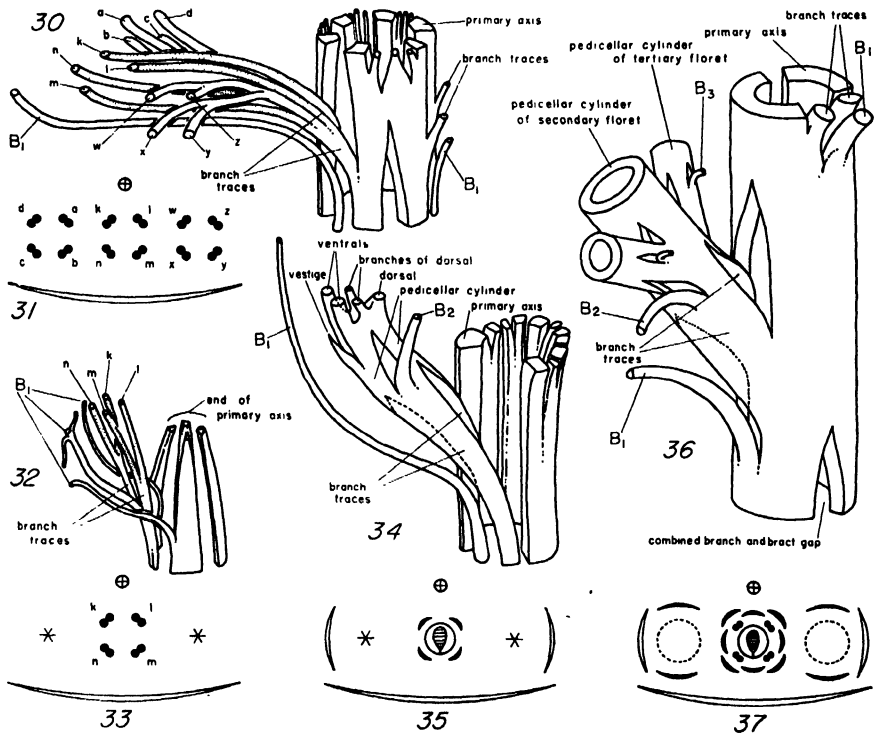
Figs. 30–37. Relationship of the vascular systems of the staminate and pistillate cymules to a simpler condition. Fig. 30. Diagrammatic representation of portion of primary axis and staminate cymule showing least modified condition. Fig. 31. Floral diagram of cymule shown in preceding figure. Fig. 32. Diagrammatic representation of terminal portion of primary axis and staminate cymule showing most highly modified condition. Fig. 33. Floral diagram of cymule shown in preceding figure. Fig. 34. Diagrammatic representation of portion of primary axis and vascular supply to pistillate cymule. Fig. 35. Floral diagram of preceding figure. Fig. 36. Generalized diagram of hypothetical ancestral type, showing portion of primary axis and vascular supply to a single three-flowered cymule. Fig. 37. Floral diagram of preceding figure.

Abbreviations used: B_1, primary bract; B_2, secondary bract; dr, dorsal; vn, ventral; tp, tepal; ves, vestigial; ped cyl, pedicellar cylinder; ov, ovular bundle; br, branch trace.

dence that there were probably at least two ovules at an earlier stage in the phylogenetic development of the flower.

The staminate inflorescence.—This consists of three-flowered cymules spirally arranged on a lax primary axis, each cymule in the axil of a large primary bract. Secondary and tertiary bracts are absent externally, nor

has internal evidence been found of their former existence in the material studied. The vascular system in the less modified staminate cymules (fig. 30) is a combination of the independent supply to a primary bract (B_1) and the two bundles (branch traces, fig. 30) of the secondary axis. The secondary axis (stippled in fig. 30) gives off vascular tissue laterally which topographically belongs to the tertiary axes. The tissue of the secondary axis, after the departure of the tertiary vascular material, continues on in the median plane to supply the stamens (k, l, m, n, fig. 30) of the secondary floret. In slightly modified cymules (fig. 24) the supply to the secondary floret has become in part associated with the supply to the primary bract and in part with that of the tertiary axes. With extreme reduction (fig. 32), the supply to the secondary floret (k, l, m, n, fig. 32) has become completely associated with that of the primary bract (B_1), while the tertiary axes are completely lacking. The anomaly exists here of bundles which resemble branch bundles in origin, contributing secondarily to the vascularization of the primary bract.

The staminate flower.—The pedicellar system of the tertiary (or lateral) staminate flowers (shown free of stippling in fig. 30) is but the single bundle which branches after moving a short distance laterally to supply the stamens (w, x, y, z, fig. 30). The pedicellar vascular system of the secondary floret (shown stippled in fig. 30) consists of the vascular tissue left after the departure of the tertiary branches. This leaves four separate traces (k, l, m, n, fig. 30), each of which may supply a stamen. Neither external nor internal evidence of tepals or pistils was found in the staminate cymules. In spite of the absence of these landmarks the disposition of the vascular tissue leaves no doubt of the presence of three florets in the average cymule.

<center>DISCUSSION</center>

Interpretation of pistillate ament, inflorescence, and floret.—Telescoping in the pistillate material of *Leitneria* has not been as great as that found in some other amentiferous plants, a fact which has much simplified the study of its vascular system.

The presence of well-defined secondary bracts below the floret suggests, by analogy with the Betulaceae (Abbe, 1935), that tertiary florets were present in the phylogenetic history of the plant. This interpretation receives even stronger support from the evidence for the presence of tertiary florets in the staminate material.

Although the floret of *Leitneria* possesses a single, simple pistil, the presence of a vestigial bundle (fig. 22, *ves* 3) suggests that another carpel may have been present. Whether the ancestral pistil was simple or compound is a question that cannot be answered on the basis of our present knowledge. It is quite obvious that the ancestral form had a definitely

superior ovary. The presence of vestiges of vascular bundles within the ovary suggests that there were once several ovules present.

The range of variation in number of tepals described in the literature is not as great as that in our material. Here, they were sufficiently abundant and so arranged as to suggest two definite cycles. When present, the vascular supply of the tepals is so rudimentary that it apparently is no longer functional.

Interpretation of staminate ament, inflorescence, and floret.—The units of the staminate inflorescence have been generally interpreted as single flowers in the axils of the bracts. The vascular anatomy of the ament supports the fact that the primary bract is a simple morphological entity. In its axil there is definite vascular evidence of three flowers cymosely arranged. This is opposed to the former descriptions which allow but a single flower in the axil of each primary bract. In the simplest cases the vascular system of the secondary axis is distinct from that of the tertiary axes. In the upper portion of the ament there is more crowding of the stamens with a corresponding reduction in number in each floret. This condition, together with anastomoses of the vascular bundles, complicates the interpretation of the relationship of the florets and their vascular supplies. This phenomenon is not unusual, however, and parallels the condition found in similar inflorescences in the Betulaceae. In the latter group of plants the inflorescences are definitely reduced from three-flowered cyme-like units. There is similar evidence of the same thing occurring in the lower parts of the aments of *Leitneria*. In the extreme terminal portion of the staminate ament, however, there has been a complete transferral of the vascular tissue of the secondary axis to the midrib of the primary bract, an extreme expression of the tendency toward fusion. In this region of the ament there is also the unusual phenomenon of the primary bract receiving supplementary vascular tissue at its margin from bundles which had an origin characteristic of branch bundles, a condition which we are unable to explain.

In summary, our investigations of the staminate material of *Leitneria* make necessary a revision of the current idea concerning the organization of the units of the staminate aments. These units are composed of three flowers instead of a single flower in the axil of each primary bract.

THEORIES CONCERNING THE RELATIONSHIP OF LEITNERIA

The systematic treatment of *Leitneria* has been quite diverse. Because of its more or less catkin-like inflorescences, *Leitneria* has been frequently included in that heterogeneous assemblage, the "Amentiferae," or its equivalent (Chapman, 1860; Cas. DeCandolle, 1864; Eichler, 1878; Baillon, 1880; Bentham and Hooker, 1880; Engler, 1894; Wettstein, 1924; Engler and Gilg, 1924; Hutchinson, 1926). It has been placed in

the Dipterocarpaceae by van Tieghem (1886; 1891), but on an erroneous basis, as was pointed out by Heim (1891; 1892). Heim (1892) suggested as an alternative to van Tieghem's proposal, that *Leitneria* is related to the Hamamelidaceae. The latter view was sanctioned by Engler (1897) with the proviso that this would hold only if *Leitneria* were considered a reduced form. Hutchinson (1926) uses essentially this same interpretation in deriving *Leitneria* from the Rosales through the Hamamelidales. Hallier, at one time (1905) also considered *Leitneria* to be a member of the Hamamelidaceae, which, however, he derived from the Magnoliales. Later, he (Hallier, 1912) placed *Leitneria* in his "Terebinthacées" which he derived from the "Proberberideae" through the Rutaceae. Finally, Bessey (1915) placed *Leitneria* directly in the Ranales.

There is little beyond taxonomic convenience to recommend the lumping of *Leitneria* with the "Amentiferae." "Naturalness" has seldom been claimed for the group, except perhaps by Linnaeus (1751). No close relationship can be hypothecated between *Leitneria*, with its hypogynous flower, and the inferior-ovaried Fagaceae, Betulaceae, and Juglandaceae. Others of the "Amentiferae," although possessing superior ovaries, differ in other respects. Thus the Salicaceae, with the exception of two species of *Populus*, have ovules with but a single integument (Schnarf, 1931) in contrast to *Leitneria* which has the two integuments exceptionally well developed (Pfeiffer, 1912). The ovule of the Myricaceae not only differs from that of *Leitneria* in having but a single integument, but differs still further in the highly vascularized state of the integument, as well as of the nucellus. Furthermore, both the Salicaceae and the Myricaceae have syncarpous pistils, a type of gynoecium from which the single simple pistil of *Leitneria* is probably not derived. *Leitneria* differs in the same respect from the Garryaceae (in which the ovules are also provided with only one integument). The inflorescence of the Garryaceae with its opposite members is in this respect even more unlike *Leitneria*, with its spirally arranged members, than are the rest of the "Amentiferae" which have been mentioned up to this point. Such comparisons across the "genetic lines" could be continued within the variable limits of the "Amentiferae." It is, however, abundantly clear that *Leitneria* is as unlike the other "Amentiferae" as many of them are unlike one another.

By adopting a broad interpretation of orders (Engler and Gilg, 1924) the more recent suggestions concerning the relationship of *Leitneria* may be summarized as follows. It has been considered a member of the:

Ranales (Bessey, 1915).
Rosales (Heim, 1892; Engler, 1897; Hallier, 1905).
Geraniales (to include part of the "Terebinthacées" of Hallier, 1912).
Sapindales (to include the other part of the "Terebinthacées" of Hallier, 1912).
Parietales (van Tiegham, 1886, 1891).

An effort to evaluate these suggestions should be made on the basis of one of Bessey's (1915) well-known dicta. This is that "plant relationships are *up and down* the genetic lines, and these must constitute the framework of phylogenetic taxonomy." It is by no means a new concept, since Bessey in an earlier paper (1897) refers the gist of it to Asa Gray. An important corollary of this principle is that plants contemporary with each other cannot be related in a direct, linear fashion. They must go back to common ancestors even in cases of the closest relationships. It is of the greatest importance that phylogenetic theories which have developed in the past few decades be applied with this corollary in mind, although it has not been the usual practice to do so.

Furthermore, if an attempt is made to consider all of the available phylogenetic evidence, there should be put into practice another basic philosophy, which is often implied, but seldom expressed. Every feature of phylogenetic significance possessed by the plant or group of plants in question must be of such nature that it may reasonably be derived from that of the hypothecated ancestral form. The pitfalls in applying this working principle are numerous, nor can they be avoided, largely because of the absence of a clear paleobotanical record for the Angiosperms. Also, the larger the group of plants taken into consideration, the less "natural" it may be, and the more difficult it is to reach definite conclusions by the use of this working principle. It is unfortunate in this particular case that *Leitneria* is a monotypic form possessing so few distinctive features. The result is that it has been put into a number of different orders whose archetypes are notably similar in most respects.

It has been found useful to think in terms of archetypes of the five orders mentioned above, insofar as these archetypes may be reconstructed on the basis of current phylogenetic theories. The sum of the more primitive characteristics for each of these orders is considered to constitute the Archiranales, Archirosales, Archigeraniales, Archisapindales, and Archiparietales, respectively.

The archetypes of all five of these orders possess the primitively woody habit (Eames, 1911; Sinnott and Bailey, 1914b) from which *Leitneria*, which is a small tree, could well have been derived.

The primitively stipulate (Sinnott and Bailey, 1914a), simple and palmately veined (Sinnott and Bailey, 1915) type of leaf whose vascular supply is trilacunar in origin (Sinnott, 1914) characterizes the archetype of each of the five orders. From this type of leaf it is easy to derive the simple, pinnately veined, exstipulate leaf of *Leitneria* with its trilacunar origin of the leaf traces.

Either the very primitive solitary flower (Parkin, 1914; Zimmermann, 1935) or relatively simple inflorescences occur in the archetypes of the

five orders. Such certainly precede the highly modified type of inflorescence found in *Leitneria*.

The much modified type of vessel member in *Leitneria* (Type IV, Bailey and Tupper, 1918) with its simple perforation plate and alternate pit arrangement on the side walls is considered more advanced than the absence of vessels in the Archiranales, the Type I vessel member in the Archirosales, Archisapindales, and Archiparietales, or the Type III vessel member of the Archigeraniales (Bailey and Tupper, 1918).

The secondary xylem of *Leitneria* (Heim, 1892; Trelease, 1895; verified by the writers) is further highly modified in having vessels arranged in radial or diagonal pore chains, in contrast with which Frost (1930) considers the diffuse porous type more primitive. The bulk of the xylem is composed of thin-walled elements with minute pits whose apertures are relatively elongate, and of some septate elements; while the primitive type of tracheary element is considered to be simple rather than septate and to have large scalariform pits (Frost, 1930). The xylem parenchyma in *Leitneria* is terminal, while diffuse parenchyma is considered more primitive (Jeffrey, 1917). The xylem rays are mostly uniseriate and heterogeneous, considered an advanced condition by Kribs (1935). So advanced is the secondary xylem of *Leitneria* in these various respects that there would seem little difficulty in deriving it from the archetypes of any of the five orders in question.

We tentatively interpret the flower of the immediate ancestor of *Leitneria* as bisexual, with a perianth composed of two cycles, at least one cycle of stamens, and perhaps a several-carpelled gynoecium. While we feel that the ancestral gynoecium was probably apocarpous, we recognize the possibility of its origin from a syncarpous one (by analogy, for instance with the tendencies in the Valerianaceae and Dipsacaceae), although there is no internal evidence to support the latter view. The floral organization of the archetypes of the five orders is either spiral or spirocyclic, and apocarpous. Tentatively any of these combinations may be considered as suitable ancestral conditions for the much reduced flowers of *Leitneria*.

The anatropous position of the ovule with the micropyle turned away from the placenta in *Leitneria* appears to provide a diagnostic feature which would serve to exclude the Archisapindales, since the latter are characterized by the reverse orientation of the micropyle when the ovule is anatropous. The other four orders may well have had a type of ovule orientation from which that of *Leitneria* could have been more readily derived.

Two extremely well-developed integuments are present in the ovule of *Leitneria*, a condition which is also to be found in the archetypes of the five orders.

The eight-nucleate embryo-sac with its ephemeral antipodals develops from a megaspore in the typical manner in *Leitneria*. The megaspore is one of four derived from a megaspore mother cell, which in turn is derived from a single archesporial cell (Pfeiffer, 1912). There is general agreement that the eight-nucleate type of embryo-sac is primitive (Schürhoff, 1926; Schnarf, 1931, 1936), but its wide distribution throughout the Angiosperms, including the archetypes of the five orders, makes it of no diagnostic significance. The relatively primitive condition of the origin of the embryo-sac from a megaspore rather than from a megaspore mother cell is common to all five of the orders being considered.

Whether the cellular type (Schürhoff, 1926) or the nuclear type (Schnarf, 1931) of endosperm is to be considered the more primitive, the presence of the nuclear type in *Leitneria* (Pfeiffer, 1912) as well as in all five of the orders renders this category of information useless.

Leitneria is crassinucellate (Pfeiffer, 1912), a condition which is considered more primitive than the tenuinucellate (Schnarf, 1936). But the archetypes of the five orders are also uniformly crassinucellate.

The large size of the suspensor in *Leitneria* (Pfeiffer, 1912) is a primitive characteristic which is not shared by the archetypes of the Sapindales and Parietales, but does characterize the archetypes of the Ranales, Rosales, and Geraniales. Except for the fact that our knowledge of the details of embryology in many families is limited to but a single species each, this might be considered an important basis for the exclusion of the Archisapindales and Archiparietales from further consideration. As it is, it provides merely a tentative reason for excluding the archetypes of these two orders as potential ancestral forms of *Leitneria*.

The large number of cells ("hundreds") in the embryo of *Leitneria* (Pfeiffer, 1912) also suggests the origin of *Leitneria* from more primitive archetypes.

The chromosome number and the development of the male gametophyte in *Leitneria* are both unfortunately unknown as far as we are aware.

Thus there is little gained of a positive nature in attempting to decide whether *Leitneria* is more likely to have been derived from the Archiranales, Archirosales, Archigeraniales, Archisapindales, or Archiparietales. The orientation of the ovule, the massive suspensor, and the nature of the young embryo, and possibly the gynoecium serve provisionally to exclude the Archisapindales from further consideration. Their slender suspensor, less primitive embryo, and possibly the structure of the gynoecium, seem also to eliminate the Archiparietales. There remain the archetypes of the

Ranales, Rosales, and Geraniales between which there is very little choice. The Ranales might be excluded because of the great changes which would have to be undergone by *Leitneria* to derive it from the Archiranalean type. This tentatively leaves the Rosales (including the Hamamelidaceae) or the Geraniales as potentially logical orders in which to leave the Leitneriaceae.

Further information concerning the Leitneriaceae (especially chromosome number and morphology, and the development of the male gametophyte) as well as a better co-ordination of the phylogenetic data for other families is needed. Perhaps then *Leitneria* may be placed with somewhat more certainty.

SUMMARY

1. The pistillate flower of *Leitneria* is composed of a single, simple, uniovulate pistil surrounded at the base with a perigon composed of three to eight diminutive tepals.

2. There is vascular evidence in the pistillate flowers which suggests the former existence of a larger number of ovules and carpels. We are of the opinion that the gynoecium is derived from an apocarpous ancestral form.

3. The pistillate flowers are solitary in the axils of primary bracts, each of which is accompanied by two secondary bracts. The pistillate inflorescence is a relatively few-flowered spike.

4. The staminate flower is composed of one to four stamens unaccompanied by tepals.

5. There is vascular evidence that three flowers occur in the axil of each primary bract of the staminate inflorescence. No secondary bracts were observed. The staminate inflorescence is a many-flowered compound ament.

6. The possibility of the origin of *Leitneria* from the archetypes of the Ranales, Rosales, Geraniales, Sapindales, and Parietales (as suggested by various writers) is surveyed. It is tentatively concluded that the Archiranales, Archisapindales, and Archiparietales would be less likely ancestral forms than the Archirosales or Archigeraniales. The Leitneriaceae is left in either the Rosales or Geraniales, and the need for more diagnostic evidence is stressed.

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Studies in the Crassulaceae: Villadia, Altamiranoa and Thompsonella

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Two recent authors, Bachni (1937) and Walther (1938), have published independently on the status of the generic names, *Villadia* and *Altamiranoa*. Essentially opposite conclusions were reached concerning the nomenclature, although both writers agreed that the species in these two genera proposed by Rose (1903) really belong together in the same genus. Bachni chose for the aggregate genus the name which has page priority, i.e., *Villadia;* Walther, by identifying the type species of *Villadia* with *Thompsonella minutiflora*, restricted *Villadia* to the two species of the former *Thompsonella* and employed *Altamiranoa* for the aggregate genus, resulting from the fusion of the rest of the species of *Villadia* with the species of *Altamiranoa* as defined by Rose.

Faced with the need of reaching a conclusion concerning which of these authors to follow, I have reviewed the available evidence. At first reading, the argument of Walther appeared entirely satisfactory and it seemed reasonable to adopt his conclusions. Further study, however, indicated certain difficulties which could not be ignored. Walther republished the original illustration of the type of *Thompsonella minutiflora* (Rose) Britton and Rose. He also reproduced a photograph of the type specimen of *Cotyledon parviflora* Hemsley, on which *Villadia* is based, from the Kew Herbarium in England. These illustrations were placed side by side by him for comparative purposes, and were claimed to represent plants of the same species. Casual observation of Walther's plate indicated this conclusion to me, but close investigation revealed differences in the orientation of the top of the inflorescence, relation of the flowers to the bracts, number and shape of cauline leaves, and presence or absence of rosette leaves. When thirteen herbarium specimens exactly matching the illustration of the type of *Cotyledon parviflora* were compared with four identical with Rose's *Thompsonella minutiflora*, still further differences were evident which could not be made out from the illustrations. The two kinds of plants were abundantly different, as is shown in the following table, in which the distinguishing characters are set forth.

Cotyledon parviflora	*Thompsonella minutiflora*
1. Petals connate for ⅓ their length.	Petals connate for ⅛ of their length.
2. Sepals glandular roughened.	Sepals smooth.
3. Flowers strictly axillary.	Flowers inserted somewhat above the subtending bracts.

4. Cauline leaves linear, terete, acute, numerous (±36).	Cauline leaves thick, ovate-oblong, few (±5).
5. Basal rosette leaves absent. (Careful examination of plants with roots failed to reveal evidence that there had been rosette leaves which had disappeared prior to collection.)	Basal rosette leaves present.
6. Flowering stem somewhat curved or nodding at tip.	Flowering stem erect.
7. Stems and leaves green.	Stems and leaves suffused with purple.

In view of this evidence, Walther's conclusions seem quite unsatisfactory and untenable, and it is necessary to reject the fourteen new specific combinations which were made by him on a basis of those conclusions. Since references were not supplied to the previously published descriptions of the species, none of these new combinations are truly valid anyway, but they are now in print to cause confusion.

For those who may wish to check the differences between the two species mentioned and to test the correctness of the above statements, I cite the specimens on which my conclusions are based. In the citations, BH represents Bailey Hortorium and NY, New York Botanical Garden.

Villadia parviflora (Hemsley) Rose. ARIZONA: San Francisco Mts., 1904, C———— (name on label is not clear) *and Lloyd,* specimens flowered at NY, July, 1905, *21179* (NY). MEXICO. Hidalgo: near El Salto, September 16, 1903, *J. N. Rose & J. H. Painter 820 and 7116* (NY). San Luis Potosi: 22° N. lat., 6,000–8,000 ft., 1878, *C. C. Parry and E. Palmer 238* (NY); from the valley, *J. G. Schaffner 383* (NY). Tamaulipas: valley near Tula, *C. G. Pringle 9637* (NY). Zacatecas: Zacatecas, *C. A. Purpus (J. N. Rose 931)* (NY). Valley of Mexico, *J. N. Rose 19184* (NY); *L. H. MacDaniels 770* (BH).

Thompsonella minutiflora (Rose) Britton & Rose. Mexico. Puebla: Tehuacan, *J. N. Rose 25662* (NY), *C. A. Purpus 19985* (NY), *M. B. Halsted* (NY).

Baehni rightfully did not confuse his discussion of *Villadia* with the *Thompsonella* problem. Under *Villadia,* he made new combinations for eight species of *Altamiranoa* and one species of *Sedum.* So far as I have had opportunity to check, these appear justifiable, particularly since the characters for separation of *Altamiranoa* and *Villadia* seem not of generic importance.

Nine specific names still remain in the now abandoned *Altamiranoa.* I am prepared to transfer one of these to *Villadia,* but feel that it is both unwise and unnecessary to publish new combinations for the others until after critical study of actual specimens to determine the specific validity of each of the entities. The one new combination that I make below is

necessary because the plant is in cultivation and requires a definite designation at once. So far as known to me, the other species concerned are not in the horticultural trade and specimens have not been available to me.

Thompsonella appears distinct from *Villadia*, but I am in no position now to consider its relation to *Echeveria*. My casual tendency is to follow Berger, who reduced it to a section of *Echeveria*, since the plants have the appearance of that genus, but I have not given careful study to the matter.

As now considered, *Villadia* Rose (*sensu latiore*) contains about twenty-five species and is capable of division into two sections, EUVILLADIA (*Villadia* Rose, Bull. N. Y. Bot. Gard. 3: 3. 1903.) and **Altamiranoa** (Rose) n. stat. (*Altamiranoa* Rose, Bull. N. Y. Bot. Gard. 3: 31. 1903.). The genus includes a group of species which are intermediate in character between *Sedum* and *Echeveria*. It is characterized by the petals somewhat connate at the base, the inflorescence terminal, the flowers small, and the absence of rosette leaves. *Echeveria* has rosette leaves, large flowers, and the inflorescence borne laterally. There are also various other minor differences which serve to distinguish these genera, but the principal ones are those given.

The Section ALTAMIRANOA differs from EUVILLADIA in having the flowers borne on one-sided racemes or cymes. In the typical section the flowers are arranged in equilateral racemes, spikes, or compact panicles. Since, for consistency, it would be necessary to divide *Echeveria* into two genera likewise, if this difference in the inflorescences were employed here as basis for generic segregation, also since it is known that this character is subject to great variation, as already remarked by both Baehni and Walther, the placing together of *Altamiranoa* and *Villadia* seems logical. Besides the character afforded by the inflorescence, the species of the section *Altamiranoa* usually have more slender roots than do those of *Euvilladia*.

As now interpreted, the section ALTAMIRANOA contains ten species. Several others will probably be shown in the future also to belong here. The species at present placed in the section are:

Villadia andina (Ball.) Baehni and Macbride, Candollea **7**: 285. 1937.

Villadia Batesii (Hemsl.) Baehni and Macbride, Candollea **7**: 285. 1937.

Villadia Berillonana (Hamet) Baehni and Macbride, Candollea **7**: 285. 1937.

Villadia Dielsii Baehni and Macbride (*Cotyledon stricta* Diels.), Candollea **7**: 285. 1937.

Villadia Dyvrandae (Hamet) Baehni and Macbride, Candollea **7**: 286. 1937.

Villadia elongata (Rose) comb. nov. (*Altamiranoa elongata* Rose, Bull. N. Y. Bot. Gard. **3**: 31. 1903).

Villadia Grandyi (Hamet) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia imbricata (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia incarnum (Ball) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia virgata (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia Weberbaueri (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.

The eight remaining species of *Altamiranoa*, some of which may also be removed to *Villadia* as a result of further study, are:

Altamiranoa alpina Fröd. Concerning this, Fröderström (1935) commented: "It is apparently a distinct species but may also be but an alpine reduced form of *A. Batesii*."

Altamiranoa decipiens (Baker) Fröd. Without specimens, I am decidedly uncertain about the proper status of this.

Altamiranoa Galeottiana Rose. According to Rose (1903) this is known only from the type locality. It should be studied very carefully before subjecting it to further nomenclatorial innovations.

Altamiranoa Jurgensii (Hemsley) Rose. This is known only from the type specimens. Fröderström (1935) made it a variety of *Altamiranoa elongata*, but without specimens, I can reach no satisfactory conclusions.

Altamiranoa mexicana (Schlect.) Rose. According to Rose this is known only from the type locality. Fröderström (1935) wrote: "A doubtful species, unknown to me."

Altamiranoa necaxana Fröd. In his original decription, Fröderström (1935) remarked that this is closely allied to *A. elongata* and perhaps only a glabrous variety of that from a less extreme region.

Altamiranoa ramulosa Fröd. This was based on Pringle's collection no. 4287. It is not clear to me why it is not an extreme variation of *Villadia Batesii*.

Altamiranoa scopulina Rose. Apparently known from the type collection only and little understood.

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Plant Responses to Carcinogenic agents and Growth Substances; their relation to Crown Gall and Cancer [1]

MICHAEL LEVINE

(WITH 34 FIGURES)

The isolation of *Bacterium tumefaciens* from wart-like growths on the stems of the Paris daisy, *Chrysanthemum frutescens,* and the production of similar overgrowths by inoculation with bacteria on a large number of species of plants, has led to the conception that these localized growths are analogous to malignant neoplasia of animals. The work of Smith (1911) who sponsored this view is well known and little need be said except to recapitulate briefly the salient features upon which these contentions were based. Smith held the view that crown gall is a malignant plant disease consisting of localized proliferation of the host cells induced by *B. tumefaciens.* The new mass of disoriented cells, at times, invaded the healthy host tissue and interfered with its normal function. The effects on the plant so infected was to cause it to become dwarfed, to lack power to form flowers and fruit, and finally to cause death.

A critical study of this disease in relation to animal cancer has been in progress in this laboratory for more than twenty years. It has been contended by the present writer (Levine, 1931–1936) that crown gall is not analogous to animal cancer. The fundamental attributes of animal cancer are dependent upon the inherent characteristics of animals. The multiplicity of cancer forms found in the animal have no analogy in the simple overgrowths found on the plant. In the absence of blood and lymph systems, metastases cannot occur in plants. The invasive character of the plant overgrowth occurs principally under certain experimental conditions. The dwarfing and death of the plant are dependent upon the site of the overgrowth. In most cases death of the plant is secondary to mechanical destruction of supporting tissues.

Cytologically, crown gall and animal neoplasia have one property in common. In both types of abnormal growth, the mass of new tissue is increased by rapid division of the stimulated or rejuvenated peripheral cells. The types of division in animal cancer are aberrant. Cells with atypical numbers of chromosomes are found which result from chromosome division without intervention of the spindle fiber mechanism. In plants, the normal process of division is similar to those found in rapidly dividing embryonic cells. Polyploid cells occur in the overgrowths due to

repeated nuclear division without cell division. The tumor giant cells in malignant animal cancer have no known origin. Malignant animal cancer is characterized by continuous growth of the new tissue with variation in the tempo of proliferation. In plants the continuity of the overgrowth is in a larger measure determined by the environmental conditions. Generally, plant overgrowths on annuals are short-lived. The tissue matures, the cells become old and differentiate forming woody structures; death follows. On perennials, subjected to seasonal changes, the overgrowths die, although the stem or branch upon which they are produced lives. Reinfection occurs with resumption of growth in the following growing season. In the case of sheltered succulent perennials, the new growths may live for a longer period, but ultimately their tissues undergo differentiation, become old, corky or leathery, and die.

Animal tumors are known to regress; the mechanism which makes this possible in the animal is entirely lacking in the plant. A wart-like overgrowth on a plant regresses by drying and shriveling. Obviously the cells of the overgrowth are not carried away by phagocytes. Yet crown gall disease is nevertheless a neoplastic disease. It undoubtedly belongs in the category of tumor diseases although its analogy to animal or human cancer is not apparent. It now appears that cancer of man and animal may arise from many causes. Experimentally, the production of cancer in animals by chemical means started with the induction of tar tumors of rabbits (Yamagiwa and Ichikawa, 1916). The production of active carcinogenic tars (Kennaway, 1924), the isolation and synthesis of 3, 4-benzpyrene (Cook, Hewett, and Hieger, 1933), the preparation of methylcholanthrene, the synthesis of 1, 2, 5, 6-dibenzanthracene (Clar, 1929), and finally the production of more than 40 chemical substances, synthesized by Fieser (1938) and his associates in America, and by Cook (1937) and his collaborators in England, have been shown to possess carcinogenic properties of greater or less potency. Styryl 430, radium, thorotrast, unrelated chemical agents, are known to produce cancer in man and animal. Endocrine products such as oestrin play an important rôle in cancer production. Cancer induced by these chemical agents are malignant growths and present cellular and clinical pictures like spontaneous neoplasia known to man and animal.

The chemicals applied locally to plants have been productive of overgrowth responses which have been described as tumors with the implication that these local excrescences may be in some way associated with malignant growths of animals.

It has been hoped that with the discovery of chemical agents as the etiological factors in cancer of animal and man, that these substances would likewise induce malignant overgrowths on plants. The early results of

application of chemical agents on plants has been reviewed (Levine, 1934). Komuro (1932) speaks of "phytoteertumors" induced on *Pisum sativum* and *Vicia faba* with tar solutions. The cytological phenomena described in the roots of these plants are suggestive of the cellular phenomena found in cancer. Havas (1939) stresses responses of plants and animals to various chemical agents as analogous. Zimmerman (1937) and collaborator, Wilcoxon (1935) showed that the application of a number of synthetic compounds,[2] most important of which is indoleacetic acid, applied to any part of a plant induces epinasty, swellings, proliferations, and roots, at the treated area. Horticulturally, these findings appear to be of economic importance.

Brown and Gardner (1936) studied the effects of 0.4 per cent suspension of indoleacetic acid and indolepropionic acid in lanolin on the bean, tomato, and sunflower. These plants responded by producing definite overgrowths. *Bryophyllum* and *Kalanchoë* produced roots only. Galls were also produced by a growth substance extracted from *B. tumefaciens* growing in media containing tryptophane. Kraus, Brown, and Hamner (1936) studied the histological effects of 0.6 per cent indoleacetic acid in lanolin on the red kidney bean grown under greenhouse conditions. They concluded that the histological development following the application of indoleacetic acid closely resembled many of those associated with crown galls produced by *B. tumefaciens*. Hamner and Kraus (1937), in a further study of the effects of a paste of indoleacetic acid (3 per cent) in lanolin to decapitated bean plants, found that these plants produce large vascular overgrowths, many of which continue to develop for a period of six months and attain a diameter of 2 cm. or more. Application of indolebutyric acid or α-naphthaleneacetic acid resulted in similar tumors on the bean plant. Roots are associated with the development of these tumors. Partially mature bean pods, when injured and treated with these agents, produce comparatively large overgrowths. Harrison's (1937) study on *Iresine Lindenii*, and Hamner's (1938) investigation of *Mirabilis Jalapa* gave results comparatively similar to those obtained with indoleacetic acid on bean plants. Beal's (1938) study of the monocotyledon *Lilium philippinensi formosanum*, *L. longiflorum*, and *L. Harrisii* are of interest since the monocotyledonous plants are resistant to the crown gall organism. The application of indoleacetic acid produces, according to Beal, two distinct types of reactions. The first two species of *Lilium* produce roots while *L. Harrisii* produces buds on application of heteroauxin. The roots formed were normally vascularized and appear to arise from the paren-

[2] α—naphthaleneacetic acid, β—naphthaleneacetic acid, acenaphthyl-5-acetic acid, indolebutyric acid, indoleacetic acid, indolepropionic acid, phenylacetic acid, and α—naphthylacetonitril.

chyma about the outer bundles. The buds arise in the cells of the epidermis and cortex in the vicinity of the leaf axil. The cytological study shows normal structures and normal cell divisions. No tumors or overgrowths were produced on these lilies.

Link, Wilcox, and Link (1937[1, 2]) made a comparative study of the effects of the crown gall organism, the extract of the organism, indoleacetic acid, and wounding on the bean and tomato plants. They contended that native growth substances can be augmented or replaced by synthetic growth substances or heteroauxin. These substances at different concentrations and amounts may produce tumors as well as those reactions characteristic of injury. Link believes that galls are possibly incited by *Bacterium tumefaciens* through heteroauxin in conjunction with other chemical agents, for *B. tumefaciens* produces indoleacetic acid when grown in media containing tryptophane. Bending of hypocotyls of bean seedlings was induced within several hours by bacterial extracts, thickening of the hypocotyls, and finally the appearance of whitish tumors adjacent to the region of application were reported. More pronounced effects were produced by heteroauxin. The effects of tryptophane (indole-a-aminopropionic acid) has not been studied. Link and Eggers' (1938) study of the hypocotyls of flax seedlings led them to believe that indoleacetic acid at varying concentrations inhibits bud initiation, but induces apical tumors, while lower concentrations retarded and diminished bud formation and decreased tumor formation.

Berthelot and Amoureux (1937) studied the effects of 1, 2, 5, 6-dibenz-anthracene, benzpyrene, indoleacetic acid as well as folliculin and allantoin on the stem of a small number of sunflower seedlings. Folliculin and benzpyrene treated stems yielded reactions, while their plants died after treatment with indoleacetic acid. In their later report (1938), they contend that indoleacetic acid reactions were analogous to crown galls obtained with *B. tumefaciens* inoculation. They claim that the crown gall organism produces indoleacetic acid in the presence of tryptophane.

Riker and his associates (1938[1, 2]) (1939) made comparisons between the physiological responses induced by inoculation with *B. tumefaciens* and those called forth by treatments with growth substances. The chemical composition of galls as contrasted with the adjacent tissue was also studied. Riker (1939) stresses the point that the great diversity of substances which call forth reactions in plants are not as important as the irritation or injury induced by them. He denies the importance of indoleacetic acid in crown gall formation and suggests that the factors which start the gall may be different from those which maintain its cellular proliferation.

The present study is a continuation of the work started a number of years ago (Levine, 1934, 1936, 1937) to induce tumors in plants by carcinogenic agents and to contrast the reactions with those induced by growth substances and by *B. tumefaciens*. Stress is laid principally on the histological structure of the heteroauxin overgrowth which consist of abortive organoids of parenchymatous tissue with feeble proliferating power. These overgrowths are short-lived and do not possess the power to grow like crown gall tissue. As biological entities in the category of neoplastic diseases, it is contended, that these new growths belong in the scale lower than crown gall. Nevertheless, indoleacetic acid under certain conditions produces small, nodular masses which present histological pictures similar to those observed in crown gall tissue. Their longevity, their power of continued proliferation, has not been found identical with crown gall tissue or malignant cancer of animals and man.

<center>METHODS</center>

The following report deals with a gross and histological study of the effects of 1, 2, 5, 6-dibenzanthracene, methylcholanthrene, 3, 4-benzpyrene, indoleacetic acid, nicotinic acid hydrochloride, sucrose, scharlach red, vitamin B_1, extracted auxin of broccoli flowers, oat leaves, and cultures of *B. tumefaciens*, *P. rhizogenes*, *P. fasciens*, and the woolly knot organisms. Twenty-one species of plants were used upon which more than 1300 treatments were made. Most of the species of plants used in these experiments had been previously studied. The species principally used in this series are *Kalanchoë Daigremontiana* Hamet and Perrier, *Bryophyllum calycinum* Salisbury and *Brassica oleracea botrytis*. Further data on *Nicotiana glauca*, sunflower, and red kidney bean are presented.

In these studies attempts were made to increase the initially stimulated growths with extracted auxin. The application of growth stimulating substances like indoleacetic acid, heteroauxin, and scharlach red were followed by treatments of extracted auxin from broccoli or oat leaves, or with crystalline B_1. These substances were suspended in hydrous lanolin (1 per cent to 3 per cent) and applied with a glass rod. Scharlach red was dissolved in ether which was applied to the area as a paint. The stems of the young plants were treated after decapitation frequently followed by pricking the cut surface with a sterile needle. The soft tissues of the stem, in many instances, were merely injured by piercing with a sterile needle. Control plants were injured in a similar fashion and were treated with ether or lanolin. Cultures of a virulent strain of *B. tumefaciens* were also used as checks on the capacity of plants to respond to the crown gall organism. Tissues at various intervals were removed and fixed in Bouin's solution, and Flemming's weaker solution. The tissues were imbed-

ded in paraffin and sectioned $7\frac{1}{2}\mu$ to 15μ. Woody tissues which resisted
sectioning were kept in the paraffin oven at 52° for varying lengths of time.
Sections were stained with Flemming's triple stain and Heidenhain's iron
alum haematoxylin.

KALANCHOË

Bacterium tumefaciens.—Young succulent plants of *Kalanchoë Daigre-
montiana* Hamet et Perrier when decapitated and inoculated with a virulent
strain of *B. tumefaciens* produce on the area treated, a small nodular over-
growth. In 45 to 50 days rudimentary leaves arise from the upper surface
of the crown gall, and an abundance of roots are formed on its lower
surface and on the adjacent tissue of the stem. Notches of the leaves
inoculated with the crown gall organism form globular masses of crown
gall tissue with no embryonic shoots, leaves, or roots as previously shown
for *Bryophyllum.* For purposes of comparison, crown galls were studied
over a period of more than a year. Frequent photographs were made
during this time to record the changes which occurred.

Scharlach red.—The effects of scharlach red in ether has already been
reported (Levine, 1939). Here it is necessary to add only the results of
further study on the development of these growths, a small number of
which behaved like those inoculated with *B. tumefaciens.* The overgrowth
shown in figure 1 was photographed about a year after treatment. The stem
on which this gall developed began to dry while the apical leaves persisted.
The gall is soft, leathery; the leafy protuberances and roots are appar-
ently dead. Microscopic study of parts of the gall six months after the
treatments were made, showed evidence of healing or regeneration. The
white tissue of the gall became covered with a greenish epidermis which
nearly covered the exposed surface. A microscopic examination of the
tissue showed an abundance of normally organized stems and roots as
in figure 2. Under high magnification typical crown gall-like tissue was
observed; woody elements were irregularly distributed through masses
of parenchymatous tissue as shown in figure 3. A more detailed study of
the softer tissues is shown in figure 4. Here uninucleate and binucleate cells
are of frequent occurrence. Isolated and disoriented clusters of xylem
tubes are shown. Surrounding this mass of active tissue are parenchyma
cells of larger dimension, many of which show an abundance of granular
substances.

Another favorable response on a *Kalanchoë* to treatment with schar-
lach red dissolved in ether, was much slower in making its appearance.
There was little reaction in the treated area for over a period of a month;
in the interim, however, the decapitated stem regenerated a new shoot.

Fig. 1. Crown gall-like structure on *Kalanchoë Daigremontiana* treated with 1% scharlach red suspended in ether, one year after treatment. ×¾.

Fig. 2. Section through the overgrowth showing organoids, six months after treatment. ×7½.

Fig. 3. Portion of tissue shown in figure 2. ×30.

Fig. 4. Portion of the same tissue under higher magnification. ×200.

Fig. 5. Another *K. Daigremontiana* with small flattened globular mass with irregular greenish protuberances, six months after treatment with 2% scharlach red in ether. Note also root formation on control treated five months previously. ×¾.

Fig. 6. Same stem showing site of roots and discrete nature of the overgrowth. ×¾.

Fig. 7. Stem shown in figure 6 one year after treatment. ×¾.

Six months after the treatment, a flattened, globular, pale greenish mass appeared which at this time was nearly ½ cm. in diameter. This was surrounded by green protuberances which appeared to be undifferentiated leaf-like structures as shown in figure 5. A few roots appear to arise from the lower surface of the gall (fig. 6). The nodes of the plant now showed long roots from which secondary roots had grown. The control treatment, which consisted of an application of lanolin after injury, showed

little effect after a month. Six months later the surface of the control area turned black, but from the healthy, internodal tissue above, long roots appeared.

The overgrowth was carefully inspected at frequent intervals and a year after treatment necrosis of the upper surface of the gall appeared as shown in figure 7. No leafy structures were finally developed. Growth of the periphery of the gall occurred only. Sections of this tissue were not

Fig. 8. *K. Daigremontiana* in which the apical node has been decapitated and the internode treated with 3% indoleacetic acid in lanolin, two and a half months previously. ×¾.

Fig. 9. Section of treated area shown in figure 8. ×30.

Fig. 10. Portion of figure 9 enlarged showing normal cortical cells from which hyperplastic cells appear to arise. ×200.

examined microscopically. Note the abundance of roots in this treated area as well as the nodes above the gall. This type of gall is not characteristic of this species for crown galls on stems of the plant invariably produce leafy structures. Current studies on *Kalanchoë* under somewhat different conditions have shown, 50 days after treatment with 2 per cent scharlach red in ether, no roots but regeneration of the decapitated stem with slight protuberances about the treated area.

Indoleacetic acid, heteroauxin.—The effects of indoleacetic acid have been studied on decapitated and injured stems of Kalanchoë. Figure 8 shows a plant decapitated and treated with a 3 per cent suspension of indoleacetic acid in lanolin. The remnant of the decapitated internode is now surmounted by small nodular masses which are characteristic of the responses reported by various workers. On microscopic examination, this tissue presents undeniable evidence of rapidly proliferating cells, not

unlike those found in the active tissue of crown gall. Here there is no evidence of roots so typical of the plants injured by needle pricks and treated with indoleacetic acid. Figure 9 shows a low power view of a section of the apical portion of this overgrowth. The major part of the tissue consists of mature, well-differentiated, parenchymatous cells. Bordering this tissue and lying on its periphery is an irregular layer of tissue consisting of embryonic-like proliferating cells, the histological nature of which is shown more clearly in figure 10. In this figure one of a number of serial sections is shown, made through the center of a protuberance. There appears to be no connection with the meristematic tissue of the host. The cells are disoriented, of various sizes, and show from one to two nuclei. Fibrovascular elements have developed, haphazardly, through the actively growing tissue of the mass. This histological structure resembles closely those described for crown gall. Should one apply the methods of tumor diagnosis employed by the animal pathologist, this tissue would be classified as crown gall. However, the clinical pictures of crown gall and those produced by indoleacetic acid are entirely different. Perhaps the most salient feature is the failure of indoleacetic acid and other growth substances studied, to endow the new cells with prolonged power to proliferate.

The decapitated pricked stems of *Kalanchoë* followed by application of 3 per cent indoleacetic acid in lanolin is followed in seven days by the appearance of roots along the internode, even though the surface of the decapitated internode only was treated. In figure 11 a plant treated twelve days previously with the heteroauxin is shown. The treated portion of the stem becomes cracked, nodules appear which rapidly degenerate or dry up.

Carcinogenic Hydrocarbons.—In contrast with the effect induced by the indoleacetic acid, the response of the Kalanchoë to the carcinogenic hydrocarbons was different. The dibenzanthracene, however, as already shown (Levine, 1939) behaved much like the indoleacetic acid in that long, branching roots are found on the treated area and occasionally small intumescences occurred. Methylcholanthrene and benzpyrene (1.5 per cent in lanolin) which are known to be very active carcinogenic agents for animals, produced necrosis of the treated decapitated internode without interfering with axillary bud development (fig. 12). Roots were sparsely produced on these young plants on the internodes below the treated area. Axillary buds below the treated area also developed in these treated plants, as shown in figure 13. The two young plants of same age and size shown in figure 14, grown under similar conditions, one of which was treated with methylcholanthrene and the other with indoleacetic acid, produced morphologically similar nodular masses on the treated internode and the methylcholanthrene specimens also produced roots.

Fig. 11. Another plant of the same species 12 days after treatment with 3% indole-acetic acid in lanolin. × ¾.

Fig. 12. Kalanchoë stems treated with carcinogenic hydrocarbons showing necrosis of treated parts, photographed two and a half months after treatment. × ¾.

Stems of *Nicotiana glauca* when injured and treated with 1, 2, 5, 6-dibenzanthracene, benzpyrene, or methylcholanthrene in lanolin and applied with a glass rod over the injured area, do not produce roots. Three months after treatment swellings and ridged surfaces are produced. Microscopic studies of these tissues show aberrant, histological structures, which show considerable hyperplasia. The sections show distortion of the fibrovascular bundles due to extra cambial proliferation, with differentia-

tion into cortical and pith cells. The pictures are those of bizarre structures with hypertrophies and hyperplasias, and yet there are characteristics which make these reaction tissues no other than responses to injury. Stems of the tomato plant treated similarly with these carcinogenic agents produce unresponsive injuries or simple calluses.

<div align="center">BRYOPHYLLUM</div>

Bryophyllum calycinum Salisbury, a species closely related to the Kalanchoë behaves unlike it in its responses to the agents used. A decapitated and injured stem of a young *Bryophyllum* (fig. 15) covered with a 3 per cent suspension of indoleacetic acid in lanolin a month previously, shows a reaction much like those observed in the sunflower. The stem cracks and numerous small root-like structures cover the surface of the treated internode. Small nodular masses occur which shrivel shortly after they are formed. The roots here are short, twisted and are not like the structures on Kalanchoë after treatment. The roots degenerate and the reaction process ceases. When the basal portion of the blade of young leaves were injured and treated with heteroauxin, plantules with comparatively long roots were formed as shown in figure 16. These leaves were young when they were treated and the photograph was made a month afterward. No nodules at the leaf base were observed in response to this treatment. Control *Bryophyllum* leaves, treated with lanolin, show no other response than scarring.

Methylcholanthrene or benzpyrene applied to decapitated and injured stems of *Bryophyllum* produce necrotic effects. The axillary bud development was not impaired. The indoleacetic acid applied to an injured portion of the stem induced small roots and slight protuberances over the treated zone as shown in figure 17. No roots were formed above or below the treated areas on these stems as on *Kalanchoë*. Sections of the indoleacetic acid treated *Bryophyllum* stems shown in figure 17 were studied. In figure 18 such a section is shown with a strand of fibrovascular bundles surrounded by parenchymatous cells, the outer layer of which appears to be atypical. Under higher magnification (fig. 19) comparatively large cortical-like cells are seen surrounding a number of irregular scalariform xylem vessels. The cells are part of a new growth which appears to have reached its maximum development. As in the *Kalanchoë*, the heteroauxin is capable of inducing slight hyperplastic tissue which matures rapidly, and appears to function only as a protective mechanism. These observations on the *Kalanchoë* and *Bryophyllum* seem to indicate that possibly too large a concentration of the carcinogenic agents was used. Yet, smaller doses have so far shown no different effect. The formation of roots and the development of the axillary buds indicate a specific host
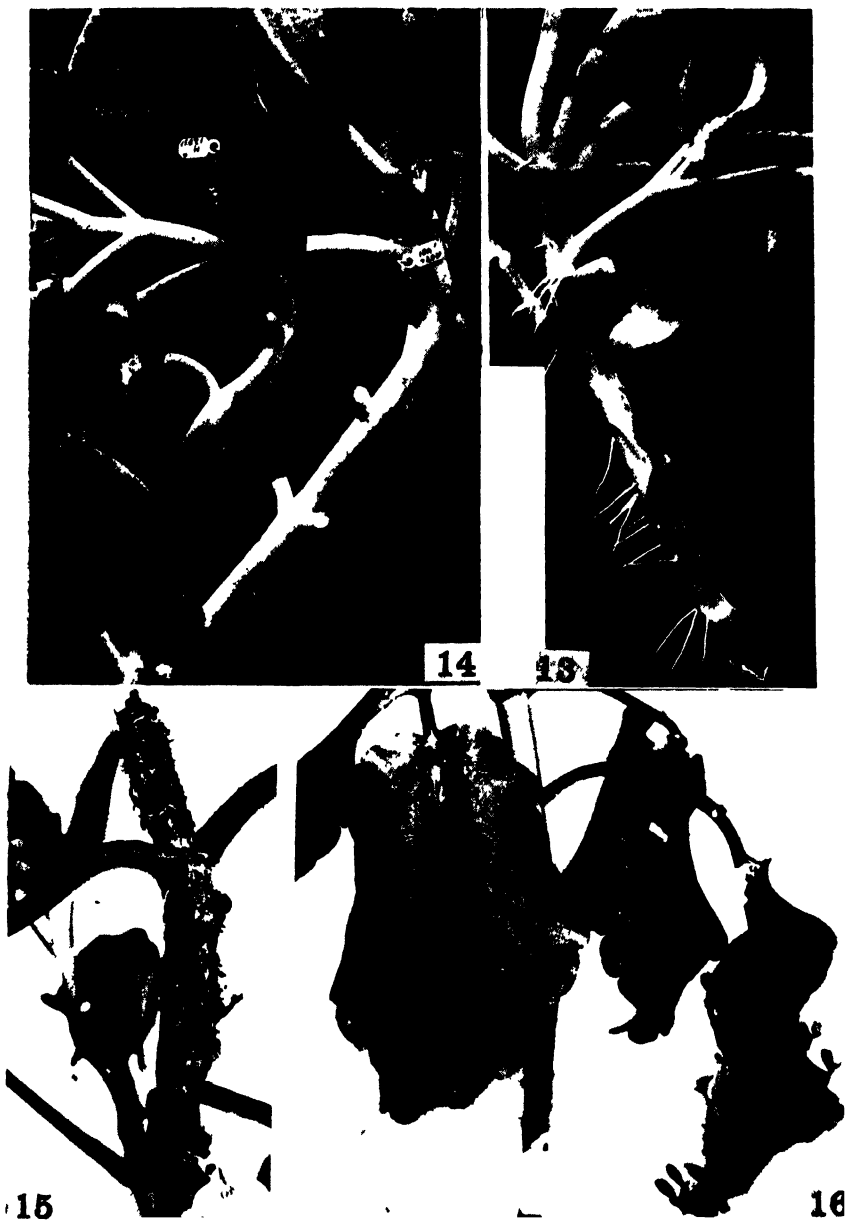
Figs. 13–14. Kalanchoe stems treated with indoleacetic acid, methylcholanthrene, and 3, 4–benzpyrine. Note root formation, two and a half months after treatment. ×¾.

Fig. 15. *Bryophyllum calycinum* decapitated and treated with 3% indoleactic acid. Note cracked stem, short roots. ×¾.

Fig. 16. Leaves of *B. calycinum* with basal portion treated after injury with 3% indoleacetic acid. ×¾.

reaction independent of the agent used. *Kalanchoë* when stimulated, even only by amputation of the apical growing point, will liberate a root form- ing substance—possibly a root forming hormone. Under conditions still unknown, the application of scharlach red and possibly indoleacetic acid cause groups of sensitive cells to proliferate forming small overgrowths which resemble histologically crown gall tissue. The general experience with the growth substances in this laboratory, shows that so-called chemi-

Fig. 17. Bryophyllum stems two and a half months after treatment with indoleacetic acid, methylcholanthrene, or benzpyrene. × ¾.

Fig. 18. Section through the reaction tissue induced by indoleacetic acid on Bryo- phyllum stem shown in figure 17. ×30.

Fig. 19. Portion of section shown in figure 18 under higher magnification. ×200.

cal tumors are small, short-lived, and lack the proliferating power which cells have when stimulated by the organism *B. tumefaciens*. From an onco-logical point of view, tumor cells possess the power of limitless prolifera-tion. When such groups of cells invade and destroy surrounding tissue, metastasize to other parts of the animal body, such tumors constitute malignant cancer. It appears from the present observations that these indoleacetic acid reactions do not fall in the category of crown gall or animal cancer. Response of cells to heteroauxin indicate a group of reac-tions more active than callus formation resulting from injury; a somewhat progressive, protective mechanism which is soon exhausted. Histologically, these small growths bear resemblance under certain conditions to crown gall tissue. It has been contended that crown gall, too, is a protective mechanism, the tissues of which proliferate because of the presence of bacteria.

<center>PHASEOLUS VULGARIS</center>

The effects of indoleacetic acid in lanolin on *Phaseolus vulgaris*, red kidney bean, have been studied intensively by Hamner and Kraus (1937). In this laboratory similar studies have been made for a number of seasons in the open garden. Young plants decapitated by removing the growing point, injured with a sterile needle, and covered with the agent, show a number of small nodular masses which form a somewhat globular structure on the treated area. On microscopic examination one notes rapid prolifera-tion and differentiation of the various tissues. Root anlagen are frequently found imbedded in the tissue. These growths are characterized by the rapidity with which they arise and the rapidity with which growth ceases. *Cleome* sp., the common spiderwart, two to three feet tall, when decapi-tated and treated with indoleacetic acid, present reactions similar to those on the bean.

Young pods of the kidney bean, when injured and treated with indole-acetic acid, produce an overgrowth in which roots have not been observed. The new growth consists of rapidly proliferating tissue in which binucleate and uninucleate cells are found. Figure 20 shows a section of the reaction tissue from a pod, 14 days after treatment with heteroauxin. In this preparation internal necrosis of the tissue has already started. The tissue dries leaving a small shriveled, tough, fibrous mass. The viable cells still show clearly well-differentiated nuclei. The induced overgrowth on these pods is short-lived and its proliferating capacity is limited. This may be associated with the natural tendency of the pod to dry with the maturity of seeds. These treated pods produce few or no seeds.

Stems of the kidney bean injured and treated with indoleacetic acid occasionally show extensive proliferation. Here, as in the pod studies,

there is an active proliferation of cells over the treated zone. The cortex and cambium appear to be stimulated; there is anisocytosis with a preponderance of hypertrophied cells. Figure 21 shows a portion of a longitudinal section of such a stem. The cortical tissue shows growth activity.
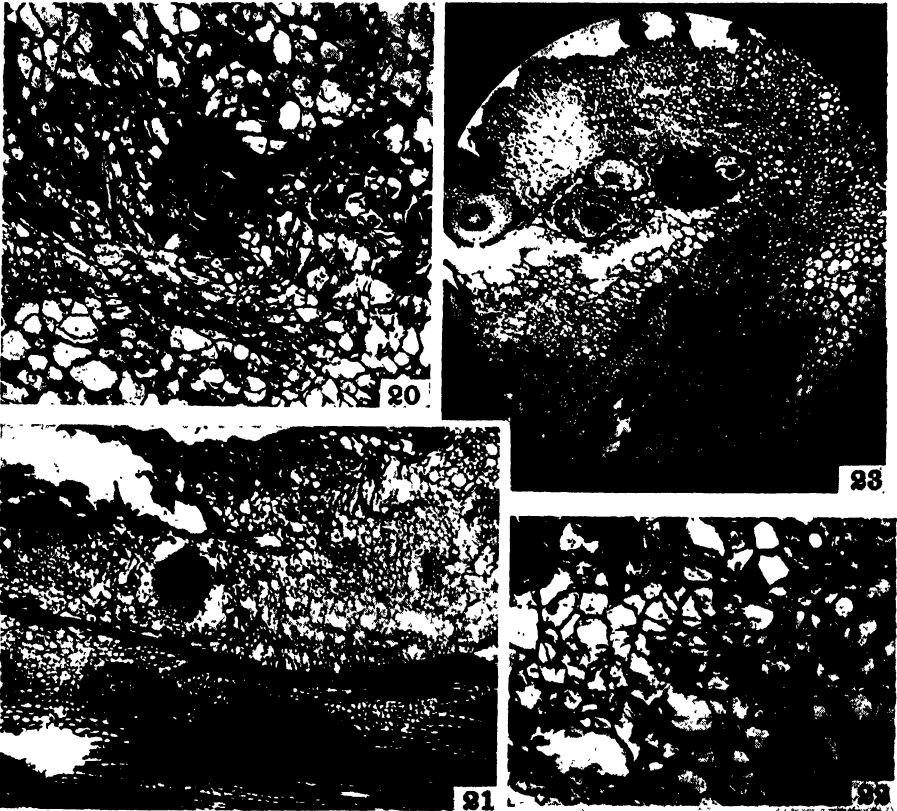
Fig. 20. Section from an overgrowth on the pod of the *Phaseolus vulgaris* treated with 3% indoleacetic acid in lanolin 14 days previously. ×200.

Fig. 21. Portion of stem of *P. vulgaris* treated as above. Note thick woody tissue and hyperplasia of cortex with root anlagen. ×30.

Fig. 22. Portion of figure 21 under higher magnification. ×200.

Fig. 23. A portion of a decapitated stem of *P. vulgaris* showing well organized roots; treated with indoleacetic acid 14 days previously. ×30.

Rudimentary roots are seen imbedded in the stimulated cortex. Breaking down of the tissue occurs within a period of two weeks after the treatment is made. Figure 22 shows a portion of figure 21 under higher magnification. The peripheral cortical cells are shrunken and take the safranin stain deeply. The more centrally placed cells show one or two nuclei. There is

evidence that there has been proliferative activity. Cell divisions have not been found at this stage.

Under more favorable conditions when treatments are made nearer the growing point, cortical proliferations abound with differentiation of tissue into well-organized root-like structures, as shown in figure 23. The predominating cells are of the cortical type, two nuclei appear in the larger cells. Here the evidence of a neoplastic disease of the crown gall type is not present.

It appears that in the reaction tissue of the kidney bean, induced by injury and application of indoleacetic acid in lanolin, there is present an increased response over that induced by injury alone. There is unquestionably a stimulus to proliferation which appears to be induced by heteroauxin. Yet these stimulated cells appears to be incapable of transmitting to the daughter cells, even to the limited extent shown by some crown gall tissue, the power to multiply. These cells stimulated, divide apparently for several generations; they differentiate and grow old, and in the absence of means for maintaining their nutrition, they die. The relationship between these reaction tissues and their effects on the host is not clear. In many instances the death of the reaction tissue occurs with the death of the stem upon which they arise. In other instances the death of the reaction tissue has no effect upon the host. The possible factor that determines the death of the treated part of the host tissue is the degree and intensity of injury which ultimately interferes with nutrition. There is no indication available to show that the new growth invades or spreads in the host tissue.

HELIANTHUS AND BRASSICA

Heteroauxin, Auxin, Vitamin B₁ and Nicotinic Acid.—The possibility of stimulating heteroauxin treated cells to greater proliferating power has been investigated. The results obtained with a limited number of agents are significant and may be mentioned at this time. It is now well known that the production of tar cancer in animals involves repeated applications of the agent. The carcinogenic hydrocarbons, however, may induce malignant neoplasia through a single injection. The studies reported previously (Levine, 1934) have shown that a single application of scharlach red or tar on *Helianthus* or *Ricinus*, appears to be as effective as repeated paintings. The newly formed cells, it seems, are incapable of further response after the first painting with the agent. Overgrowths comparable with crown gall were not produced.

The immature inflorescences of broccoli, young leaves of the oat, apical shoots of hollyhocks, were extracted with acidulated chloroform. The residue, after drying *in vacuo*, was weighed and 150 mg. to 200 mg. of

Fig. 24. Sunflower stems treated with 3% indoleacetic acid three times at intervals of 12 days and eight days—fixed two weeks after the third treatment. ×¾.

Fig. 25. Section of the stem through the treated area shown in figure 24. ×7½.

Fig. 26. Portion of figure 25 showing organoids. ×30.

Fig. 27. Basal portion of a structure shown in figure 26. ×200.

each was mixed with 5 gm. of lanolin. These agents were applied at varying intervals to stems of sunflowers, castor bean, and tomato plants treated
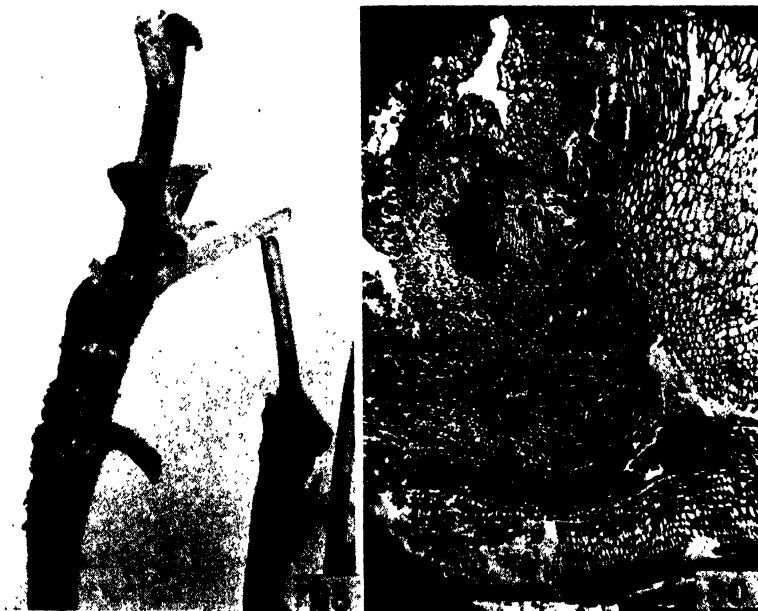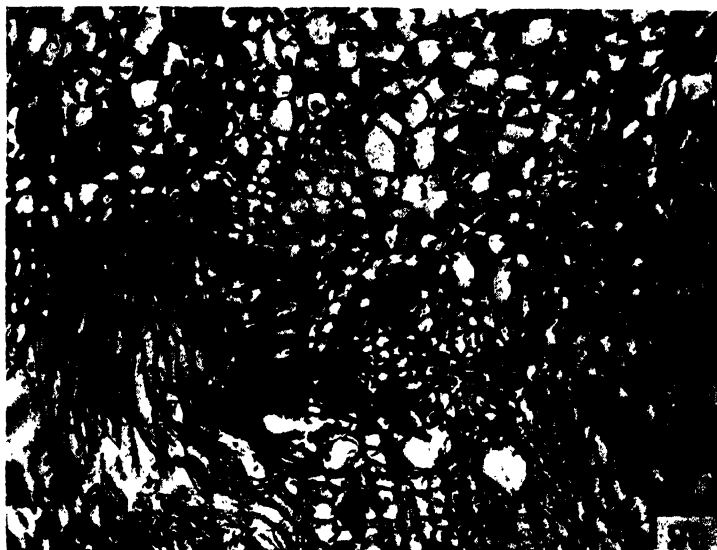
Fig. 28. Stems of sunflower treated with 3% indoleacetic acid followed by two application of vitamin B_1 in lanolin, 12 days and 8 days apart. Fixed two weeks after last treatment. $\times \frac{3}{4}$.

Fig. 29. Section from the stem on left shown in figure 28. $\times 200$.

Fig. 30. Sunflower stem treated with lanolin after apical injury fixed 53 days after treament. $\times 30$.

with 3 per cent indoleacetic or scharlach red in ether. In subsequent studies crystalline vitamin B_1, and nicotinic acid hydrochloride were rubbed up with lanolin to make a 1.2 per cent to 1.8 per cent suspension. These were used on plants after lanolin indoleacetic acid applications had been made after injury. The auxin and the nicotinic acid suspension proved ineffective and were discontinued. Figure 24 shows two sunflower stems treated with 3 per cent indoleacetic acid in lanolin. This was followed, 13 days later, by a like treatment with indoleacetic acid. A week later a similar application was made. At the time the second application of heteroauxin was made, there appeared to be a cessation of growth activity of the treated area. Following the second application, new organoids or club-shaped structures appeared. Many of these resembled root-like structures. This activity became quiescent and after applying the heteroauxin for the third time, there again appeared new organoids. The photograph was taken 36 days after the first treatment. The overgrowths are raised above the surface of the stem.

A portion of a cross section of one of the stems through the treated area is shown in figures 25 and 26. The pith shows evidence of growth disturbances induced by cell proliferation. The wood is increased in thickness and the cortex has been invaded by strands of fibrovascular elements. Club-shaped bodies consisting of parenchymatous tissue together with strands of definitely oriented fibrovascular elements seem to have arisen from the outer surface of the fibrovascular bundles. These structures branch and resemble the calloid structures on tobacco hybrids (Levine, 1937). Examination of the tissue at the base of the organoids, reveals small cells of embryonic type (fig. 27) arising from much larger parenchymatous cells.

Brassica oleracea botrytis treated on two occasions over the same area with indoleacetic acid in lanolin show interesting results comparable with those mentioned above. Figure 31 shows two stems of Italian broccoli, one of which was decapitated and pricked with a sterile needle on the cut surface and then covered with heteroauxin-lanolin paste. This treatment was repeated three weeks later and the tissue was fixed two weeks afterward. The other plant was injured similarly at the base of the stem and treated only once with the same paste and fixed two and one-half months after treatment. The amputated stem shows numerous nodular bodies which consolidated into a flattened globular mass. Microscopically, this mass consists of parenchymatous bodies in which few vascular elements are seen (fig. 32). The reaction at the basally treated plant shown in figure 31 consists of comparatively long, dried roots with small knob-shaped protuberances. On sectioning this tissue, many disoriented organoids were found as shown in figure 33. Some were long, stem-like struc-

Fig. 31. Stems of broccoli decapitated and treated twice with 3% indoleacetic acid three weeks apart. Stem to the left treated at base once with paste of indoleacetic acid in lanolin, after being injured. ×¾.

Fig. 32. Section of decapitated broccoli shown in figure 31, 14 days after last treatment. ×30.

Fig. 33. Section of basally treated broccoli shown in figure 31. ×30.

tures, others consisted of short, thickened structures composed of parenchymatous cells similar to those shown in figure 32. The double treatment of the decapitated stem seems to have affected the size of these reactions. This increased size, however, was due to the stimulation of the host tissue. Cells once stimulated appear to be little influenced by repeated treatments.

Figure 28 represents two sunflower stems injured and treated with 3 per cent indoleacetic acid and followed by an application of vitamin B_1 in lanolin two weeks later. Another treatment with the vitamin was made two weeks after the second treatment. The tissue was fixed 36 days after treatments began. Here as in the repeated indoleacetic acid treated stems, there were no added stimulations to the reaction tissues. New structures seemed to arise. Figure 29 is a section of the stem shown in figure 28. The tissue consists of cortical cells in which protoxylem-like cells are present. These elongated members are possibly the precursors of fibrovascular elements. This tissue presents no unusual appearance other than that of a callus. There is apparently no marked difference between the multiple indoleacetic acid treated plants and those subjected to heteroauxin followed by application of vitamin B_1.

Sunflowers used as controls were treated with hydrous lanolin after injury. Figure 30 shows a section through the area of treatment of such a stem made 53 days after the application of lanolin. There is callus formation with limited new growth. New or distorted fibrovascular bundles are seen with proliferations of the wood and cortex. Lanolin has a distinct protective value and the injured tissue appears to be able to respond better under the influence of a covering of lanolin than without it.

SALIX FRAGILIS

The contention that the action of *Bacterium tumefaciens* on plants grown in a solution containing tryptophane is similar to the action produced by indoleacetic acid is held by Brown and Gardner (1936), Berthelot and Amoureux (1938), Link (1937[2]) (1938). The differences in the response resulting from inoculation of *B. tumefaciens* and the reactions induced by the application of indoleacetic acid appear to be overlooked. Riker (1939) has called attention to the similarities in reactions due to inoculation with *B. tumefaciens* and treatment with indoleacetic acid.

The following experiment used to test the root producing ability of an organism or chemical is of interest, and seems applicable here. Willow branches (*Salix fragilis*) removed from the tree either in winter or summer, when stripped of leaves, cut into convenient sizes, and placed under bell jars over water, produce shoots from the apical end of the stick and roots at the basal end. The application of indoleacetic acid to the apical end of the stick as shown by Fischnich (1938) for *Populus nigra* var. *pyramidalis* and repeated here on *Salix fragilis*, shows the formation of roots along the length of the cutting, with complete suppression of shoots. Other synthetic growth substances give similar results. The application of a virulent culture of *B. tumefaciens* grown in bean agar, to the apical cut surface of these willow sticks results in shoot formation from the apical

Fig. 34. Sticks of *Salix fragilis* treated apically: $\times \frac{3}{4}$.

    1st—Cut surface covered with active culture of *B. tumefaciens*.
    2nd—Both upper surfaces of split stem covered with lanolin—apical shoots.
    3rd—Left half split stem covered with lanolin-apical shoots; right half covered
         with lanolin paste with indoleacetic acid—apical roots.
    4th—Lanolin control.
    5th—Woolly knot organism.
    6th—*Phytomonas rhizogenes*.

leaf scars and roots at the basal end. *P. rhizogenes*, the woolly knot organism, and lanolin controls showed similar results (fig. 34). There is apparently no interference with the normal tendency of the sticks to produce shoots apically and roots basally. The application of a mixture of a culture of *B. tumefaciens* (400 mg.) and tryptophane (9 mg.) to the apical cut surfaces of a number of willow sticks, suspended in a moist chamber produced only roots with abundant lenticular proliferations. In five to seven days the sticks show responses similar to that induced by the application of indoleacetic acid in lanolin alone. The application of a mixture of bean agar or an equal quantity of lanolin with tryptophane (3 per cent) was next applied to willow sticks and placed in moist chambers. Five to seven days later, the sticks produced normal leaf shoots at the apical end and roots at the basal end. *B. tumefaciens* apparently acted on the tryptophane forming a root stimulating substance like indoleacetic acid. It appears from this test that *B. tumefaciens* grown in white bean agar does not effect the normal course of shoot development in the willow cuttings. The reaction of the crown gall organism grown in tryptophane may be that of a root stimulating substance, indoleacetic acid.

Roots appear on crown galls on plants which have a tendency to form roots. Tobacco, *Nicotiana tabacum*, produces crown galls with numerous leafy shoots, while *Kalanchoë* and *Bryophyllum* stems produce crown galls with both roots and shoots.

It would appear that the host rather than the inciting organism determines the nature of the response. There is no evidence adduced to show that the mechanism in crown gall formation is due to the presence of indoleacetic acid. Here and in material previously presented, it has been shown that the response of plants to application of indoleacetic acid is primarily one of root formation in susceptible hosts. Limited hyperplasia and hypertrophy occur in the tissue response but these cells are not endowed with proliferating power sufficient to produce overgrowths comparable with crown gall. Under certain conditions, in the *Kalanchoë*, the application of scharlach red has induced crown gall-like structures. In this same species and others reported above, indoleacetic acid produces tissue responses which present histologically the tissue characteristics of crown gall. The gross morphological manifestations do not appear to be comparable.

The suggestion that these responses on plants induced by chemical agents and injury are tumors, cannot be accepted unless the plant tumor concept is different from that imposed by the animal pathologist. However, some of these reactions appear to be more than simple callus formations. They are composed of hypertrophied and hyperplastic cells forming an aberrant organization yet with limited power of proliferation. From these

facts it is conceivable that these chemical responses may be placed in the category of neoplastic diseases in a grade lower than crown gall.

SUMMARY AND CONCLUSIONS

The data presented deal with the attempt to produce cancerous growths on plants by means of carcinogenic agents or growth substances. This report covers the results of experiments for a period of two years during which many species of plants were used, principally, *Kalanchoë*, *Bryophyllum*, sunflower, kidney bean, tobacco, and broccoli. These plants were treated with certain carcinogenic hydrocarbons or other substances such as scharlach red, heteroauxin, auxins, and vitamin B_1. Repeated treatments of indoleacetic acid, and indoleacetic acid followed by treatment with vitamin B_1 were also employed.

Scharlach red which has been reported carcinogenic for certain laboratory animals has been found active in some cases with *Kalanchoë Daigremontiana*. The application of 1 per cent of this dye in ether to the apical internode after decapitation produces overgrowths which resemble crown galls. Other carcinogenes like 1, 2, 5, 6-dibenzanthracene, 3, 4-benzpyrene, methylcholanthrene induce necrosis of the treated zone. Roots, subsequently, appear in the internodal spaces below the treated areas in *K. Daigremontiana*. *Bryophyllum calycinum* treated, similarly, failed to produce roots.

The effects of indoleacetic acid in lanolin on decapitated and injured stems induces root formation. The stems crack, and small nodular masses are formed. Small overgrowths on decapitated kalanchoës present histological pictures which are identical with crown gall. In the most abundant overgrowth found so far, described by Hamner and Kraus (1937) and reported here, the heteroauxin treated pods of kidney bean present microscopical pictures very much like that found in the crown gall, but the life of the new growths are comparatively short.

Repeated treatment of stems of sunflower or broccoli with indoleacetic acid or indoleacetic acid followed by vitamin B_1, produces raised overgrowths which consist of calloid structures made up of parenchymatous tissue as well as root-like structures. These treatments fail to produce excessive overgrowth.

The fundamental difference between the heteroauxin induced overgrowth and crown gall is the limited proliferation power of the former. The chemically stimulated cells perpetuate themselves for only a few cell generations. In the most active indoleacetic acid overgrowths, cell proliferation is limited, differentiation rapid, and life of the tissue comparatively short. *Bacterium tumefaciens* under favorable conditions, induces a variety of discrete overgrowths, of which the globular type is most common.

Leafy crown galls and crown galls with roots represent other forms. The gall itself consists of parenchymatous tissue of the embryonic cell type. Longevity of this tissue is comparatively great and differentiation occurs over a long period, ultimately causing woody and corky tissue, and death. No experimental evidence has been adduced to show that the crown gall cell can proliferate in the absence of *B. tumefaciens*. Histologically, crown gall and some of the chemically stimulated overgrowths appear to be alike. Their gross morphological structures are widely different.

Reaction of plants to the crown gall organism and chemical agents are protective mechanisms comparable only to inflammation in animals and man. The proliferating power of the cancer cells is limitless. This results in invasion of normal tissue and metastatic secondary tumors. Transplantation of cancer tissue is possible for many transplant generations. The ability of these chemically induced reactions to transplant has not been attempted. Crown gall tissue has limited transplantability as contended by Jensen. The graft mechanism is complicated by the presence of *B. tumefaciens* in the inoculum.

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Additions to Florida Fungi—IV

WILLIAM A. MURRILL

Work on plant diseases in Florida is still only preliminary, in spite of all the excellent things that have been accomplished; and this is particularly true of diseases caused by the basidiomycetes. Many of the species in this large group are still unknown and the harm they do still unsuspected. A good illustration of this may be found in *Corticium, Thelephora, Hydnum, Merulius,* or *Poria.*

Among the larger polypores, which have probably received most attention, *Fomes marmoratus* and *F. supinus* are exceedingly abundant on hardwoods; *F. Curtisii* and *F. lucidus* on oak, maple, ash, etc.; *F. Calkinsii* is frequent on live-oak; *F. annosus* on pine; and *F. tornatus* on a variety of trees. *Fomes geotropus* still presents a problem, occurring as it does on several hardwoods and also on cypress. *Polyporus hispidus* is all too common on oaks, and *P. ludovicianus* is fully as threatening, appearing frequently on shade trees along city streets. *P. sulphureus* is another common and destructive tree parasite, which even occurs in South America. *P. fissilis* attacks the trunks of species of oak, *P. persicinus* the roots of the live-oak, and *P. Schweinitzii* the roots of various pines.

Idle and meaningless words, most of them; for what do we really know about the life history and effects of these fungi on the trees in Florida? Pathologists have always been glad to accept assignments to this state during the winter, when most things are dormant, but they rush to get out before real activity begins. There is still a vast opportunity for the patient investigator here, where the forest will always be a dominant factor.

When we turn to the gill-fungi, *Clitocybe tabescens* looms big. There is scarcely a tree or shrub which it will not attack. I have seen magnificent shade trees wilt and die without apparent cause until tell-tale mushrooms sprang up about their base. *Armillaria mellea* is also active but the sporophores are rarely seen. Sometimes a large crop will come out in midwinter. *Lentinus lepideus,* like other members of its large group, thrives under subtropical conditions. I have seen it all the way to Buenos Aires. *Schizophyllus alneus* is one of the fastest-working agarics I know. It has to be to fruit on a rotten apple. *Pleurotus ostreatus* is very abundant in Florida, as are species of *Flammula* and the bitter clusters of *Hypholoma fasciculare* springing up from the roots of trees.

Enough has probably been said to suggest the importance of more work on the Florida fungi. During the past few years I have been attacking the problem in a taxonomic way, devoting particular attention to Alachua County, situated near the center of the state in a region rich in both pine-

lands and hammocks. The numbers cited in the following discussion of new species from this region represent collections in the Herbarium of the Florida Agricultural Experiment Station, at Gainesville, where Mr. Erdman West is mycologist, and all my work has received his enthusiastic support.

Coltricia Mowryana sp. nov.

Pileo flabelliformi, 7–10 cm. lato, multizonato, fulvo, lobato; tubulis casta-neis, angulatis, 5–8 mm. longis; sporis fulvis, 8–9 × 4–5μ; stipite eccentrico, fulvo, tomentoso, 2–4 × 1 cm.

Pileus flabelliform, plane to slightly depressed, gregarious, 5–8 × 7–10 × 0.5–1 cm.; surface radiate-sulcate, multizonate, innate-radiate-fibrillose, shin-ing, fulvous; margin lobed, isabelline in younger stages, sterile for about 2 mm.; context very thin, fibrous, tough, fulvous; hymenium slightly determinate-decurrent, even to somewhat rough and pitted with age, castaneous to fuliginous in mature specimens, ferruginous on the sterile marginal band; tubes entire, angular, thin-walled, 5–8 mm. long, 3 to a mm.; spores ellipsoid or ovoid, smooth, fulvous, granular, 8–9 × 4–5μ; cystidia none; stipe eccentric, equal, cylindric, densely velvety-tomentose, fulvous, 2–4 × 1 cm.

Type collected by W. A. Murrill in the decayed hollow trunk of a living red bay, *Persea borbonia* Spreng., in Sugarfoot Hammock, near Gainesville, Fla., Nov. 7, 1938 (*F 18391*). Also collected by the author on a rotten log of red bay in South Planera Hammock, eleven miles north-west of Gainesville, Oct. 30, 1938 (*F 18375*). Rarely seen and probably confined to this one host. Practically all the trees of this species in the vicinity of Gainesville are hollow and partly decayed. This polypore may be the active agent. Another species often found here in the hollow trunks of red bay is *Hapalopilus licnoides* (Mont.) Murrill, but it grows abun-dantly on various kinds of dead wood. Mr. Harold Mowry, to whom this interesting new species is dedicated, is Director of Research in the Florida Agricultural Experiment Station.

Gymnopilus subdryophilus sp. nov.

Pileo convexo-subexpanso, 5–6 cm. lato, fulvo, praefelleo; lamellis sinuatis, latis, sporis 5–6 × 3–4μ; stipite flavido, 4–6 × 0.3–1 cm.

Pileus convex to subexpanded, gregarious to cespitose, 5–6 cm. broad; surface becoming smooth and glabrous, fulvous, margin even, entire; context very bitter at once; lamellae sinuate-decurrent, broad, rather crowded, inserted, entire, ochroleucous to ferruginous, at length fulvous; spores ellipsoid, smooth, ferruginous, 5–6 × 3–4μ; stipe tapering upward, smooth, glabrous, whitish-

myccelioid at the base, pale-yellowish, 4–6 $\times$ 0.3–0.5 cm., reaching 1 cm. at times at the base.

Type collected by W. A. Murrill on an oak log near Magnesia Springs, Fla., May 27, 1938 (*F 16226*). Also collected by E. West on an oak log at Newnan's Lake, July 7, 1938 (*F 17486*). Not rare on oak logs about Gainesville. It is not scaly like *G. dryophilus* Murrill and the taste is exceedingly bitter instead of mild. From *G. amarissimus* Murrill it differs in growing on hardwood and having much smaller spores.

Galerula alachuana sp. nov.

Pileo conico-convexo, 5–7 mm. lato, striato, avellaneo-isabellino; lamellis adnatis, sporis 12–14 $\times$ 7–8μ; stipite stramineo, 6 $\times$ 0.1 cm.

Pileus conic to convex, gregarious, 5–7 mm. broad; surface dry, glabrous, striate, avellaneous-isabelline, isabelline on the small umbo, margin straight, entire; lamellae adnate, ventricose, broad, inserted, medium distant, entire, fulvous, with white edges; spores ellipsoid, smooth, granular, deep-ferruginous, 12–14 $\times$ 7–8μ; cystidia none; stipe tapering upward, smooth, glabrous, stramineous, about 6 cm. long and 1 mm. or less thick.

Type collected by West, Arnold and Murrill in moist soil under hardwood trees at Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18326*). Also collected by the same persons on the ground in Sugarfoot Hammock, Oct. 18, 1938 (*F 18318*). Suggesting *G. tenera* (Schaeff.) Murrill and having similar spores but differing in several ways. It never occurs on lawns but only in low, wet hammocks.

Naucoria appendiculata sp. nov.

Pileo late convexo, 1.3 cm. lato, isabellino, striato; lamellae adnexis, albo-fimbriatis, sporis ellipsoideis, 6 $\times$ 3–4μ; stipite pallido isabellinoque, 4 $\times$ 0.1 cm.

Pileus broadly convex, solitary, 1.3 cm. broad; surface dry, glabrous, isabelline, subfulvous on the disk, margin entire, striate, appendiculate; context membranous; lamellae adnexed, rounded behind, broad, medium distant, inserted, fulvous, the edges white-fimbriate; spores ellipsoid, smooth, pale-ferruginous under the microscope, 1–guttulate, about 6 $\times$ 3–4μ; cystidia none; stipe equal, smooth, finely fibrillose and pallid above, squamulose and concolorous below, 4 $\times$ 0.1 cm.

Type collected by West, Arnold and Murrill on an oak log in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18367*). The spores are doubtless fulvous in mass, the color of the mature gills. The small veil does not leave a ring.

Hebeloma floridanum sp. nov.

Pileo convexo-expanso, umbonato, 3.5 cm. lato, viscido, stramineo; sporis ovoideis, 8 × 5μ, cystidiis 40 × 15μ, stipite albo, 5 × 0.5–0.6 cm.

Pileus convex to expanded, umbonate, gregarious, 3.5 cm. broad; surface viscid, smooth, shining, glabrous, stramineous, margin even, entire; context white, unchanging, without characteristic odor or taste; lamellae adnexed with decurrent tooth, ventricose, medium broad and medium distant, inserted, pallid to discolored, edges fimbriate; spores ovoid, smooth, ferruginous, 1–guttulate, about 8 × 5μ; cystidia bottle-shaped, hyaline, blunt and crested at the tip, projecting about 40 × 15μ; stipe equal, smooth, shining, glabrous, white, furfuraceous at the apex, 5 × 0.5–0.6 cm.

Type collected by W. A. Murrill under hardwoods in a high hammock at Gainesville, Fla., Oct. 17, 1938 (*F 18365*). Having the usual appearance of *Hebeloma* with cystidia like those of *Inocybe* and spores resembling those of *Cortinarius*. They are umbrinous in mass and ferruginous under the microscope.

Crepidotus praelatifolius sp. nov.

Pileo dimidiato, gregario, 1–2 mm. lato, albo, piloso; lamellis praelatis, sporis globosis, 6μ.

Pileus fleshy, sessile and dimidiate or conchate to resupinate, densely gregarious, imbricate, often laterally confluent, 1–2 mm. broad; surface white, unchanging, covered with long, white, delicate hairs, margin even, entire; context white, membranous, becoming inconspicuous at maturity; lamellae very few, very broad, entire, pallid to fulvous, becoming folded and irregular with age; spores globose, smooth, yellowish-brown, about 6μ.

Type collected by A. S. Rhoads on the bark of a dead magnolia log in Gainesville, Fla., Sept. 8, 1938 (*F 18107*). A very peculiar species, apparently related to *C. latifolius* Peck and *C. parvulus* Murrill. The tiny caps are little more than tufts of hairs holding the few large gills in position until the spores mature. Later, the gills become more prominent and little else can be seen on the substratum.

Entoloma subalbidum sp. nov.

Pileo convexo-subplano, 3–6 cm. lato, avellaneo vel albo, farinaceo; lamellis confertis, sporis angulatis, 8–10μ; stipite albo, glabro, 5–7 × 0.6–0.8 cm.

Pileus convex to nearly plane, gregarious, 3–6 cm. broad; surface smooth, glabrous, opaque and pale-avellaneous when fresh and moist, white and shining when losing the moisture, avellaneous in the herbarium; margin incurved, even and entire, rimose at times with age; context whitish, opaque, with strongly

farinaceous odor and taste; lamellae sinuate, narrow, crowded, inserted, broadest behind, uneven, toothed, white to pink; spores decidedly angular, apiculate, 1–guttulate, pink, 8–10μ; cystidia none; stipe equal or tapering upward, smooth, glabrous, white, shining, 5–7 × 0.6–0.8 cm.

Type collected by West and Murrill on the ground under hardwood trees in South Planera Hammock, about eleven miles northwest of Gainesville, Fla., Oct. 26, 1938 (*F 18311*). Suggesting *E. albidum* Murrill and also near *E. Grayanum* (Peck) Sacc. Found in abundance, some of the drier hymenophores being milk-white and shining, while others were hygrophanous on the margin and still others opaque and avellaneous over the entire surface. After a few hours, however, in the electric oven, they all took on the same avellaneous shade.

Russula clitocybiformis sp. nov.

Pileo convexo-praedepresso, 4.5 cm. lato, albido, subtomentoso, sapore grato; sporis globosis, albis, 9–11μ, stipite albo, 3 × 0.8 cm.

Pileus convex to deeply depressed, solitary, 4.5 cm. broad; surface slightly viscid, finely tomentose, dirty-white, margin even, entire, strongly deflexed on drying; context very thin, white, unchanging, odorless, mild or nearly so; lamellae adnate, some forking at the base, narrow, rather close, inserted, entire, thin, white, unchanging; spores globose, spinulose, white, 9–11μ; sterile cells abundant, spinulose, sharp, smooth, hyaline, about 60–75 × 5–10μ; stipe equal, smooth, glabrous, white, unchanging, 3 × 0.8 cm.

Type collected by West, Arnold and Murrill under hardwood trees in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18366*). Having the appearance of a white *Lactaria* or *Clitocybe* when dried. A rare and interesting species.

Russula regalis sp. nov.

Pileo convexo-subdepresso, 9 cm. lato, vinoso, glabro, sapore grato; lamellis latis, adnatis, sporis ochraceis, echinulatis, 7–9μ longis; stipite albo, 3 × 1.5–2 cm.

Pileus convex to expanded, slightly depressed, solitary, 9 cm. broad; surface glabrous, polished, vinosous, slightly viscid, margin somewhat striate; context very thin, white, unchanging, odorless, mild; lamellae adnate, very broad, not depressed behind, a few forked behind and very few inserted, medium distant, fimbriate, becoming luteous at maturity; spores deep-yellow, subglobose to broadly ellipsoid, prominenty echinulate and somewhat reticulate, 7–9μ long; cystidia none; stipe slightly tapering downward, smooth, white, unchanging, glabrous, 3 × 1.5–2 cm.

Type collected by Dwight Lucas under oaks in Gainesville, Fla., Nov. 8, 1938 (*F 18371*). The luteous gills and purple cap make a royal color combination rarely displayed so vividly.

Russula rubrifolia sp. nov.

Pileo convexo-depresso, 9 cm. lato, atropurpureo, praefelleo; lamellis latissimis, adnatis, sporis globosis, albis, tuberculatis, 6–8μ; stipite roseo, 4.5 × 1.5–2 cm.

Pileus convex to deeply depressed, solitary, 9 cm. broad; surface somewhat viscid, pruinose to glabrous, atropurpureous or badious, margin even, undulate, not peeling at all; context thin, white, unchanging, odorless, very bitter at once; lamellae squarely adnate, some forked at the base, equal, ventricose, unusually broad, 1.5 cm. at least, entire, bright-red on the edges for their whole length; spores globose, white, 6–8μ, decorated with scattered warts, some of them elongate like a cock's comb; cystidia none; stipe tapering downward, smooth, glabrous, rose or incarnate, solid, white within, unchanging, 4.5 × 1.5–2 cm.

Type collected by W. A. Murrill on the ground in a forest of longleaf pines near Orange Heights, Alachua Co., Fla., Nov. 9, 1938 (*F 18387*). Suggesting large forms of *R. uncialis* Peck but with different habitat, color, taste, and gill characters. It is a beautiful and striking species, highly colored, with firm flesh, and drying without much change. Microscopic characters indicate a close relationship with *R. uncialis* and *R. purpurina*.

Lepiota phaeostictiformis sp. nov.

Pileo convexo-expanso, umbonato, 1.5–2 cm. lato, atro-squamuloso; sporis ellipsoideis, 5–6 × 3–4μ, stipite albo, pruinoso, 4–5 × 0.2–0.3 cm.; annulo albo et fusco.

Pileus convex to expanded, mammillate, gregarious to subcespitose, 1.5–2 cm. broad; surface dry, white with black scales, black on the broad disk, margin even, entire; context thin, white, unchanging, odorless; lamellae free, rounded behind, ventricose, rather broad and rather crowded, finely fringed, white, unchanging; spores ellipsoid, smooth, hyaline, 1–guttulate, obliquely apiculate, 5–6 × 3–4μ; stipe tapering upward from a somewhat clavate base, smooth, finely pruinose, white, unchanging, 4–5 × 0.2–0.3 cm.; annulus 1 cm. from the apex, fixed, persistent, double, the upper margin white and fimbriate, the lower membranous and fuscous.

Type collected by West, Arnold and Murrill on a rotten pine log in Prairie Creek Hammock, a few miles southeast of Gainesville, Fla., July 15, 1938 (*F 17839*). Also collected by W. A. Murrill on rotten pine wood in

a low hammock at Gainesville, Nov. 1, 1938 (*F 18325*). Closely related to *L. phaeosticta* Morgan, found on a log in Ohio.

Hydrocybe subminutula sp. nov.

Pileo convexo, 7–10 mm. lato, viscido, rubro; lamellis decurrentibus, latis, flavidis; sporis 5–6 × 3–4μ; stipite rubro, 1.5–2.5 × 0.1–0.2 cm.

Pileus convex to subexpanded, rarely depressed, gregarious, 7–10 mm. broad; surface viscid, smooth, glabrous, red, soon fading to yellow but often retaining the red color in the center, margin even, entire; lamellae arcuate, decurrent, distant, broad, inserted, entire, pale-yellow; spores ellipsoid, smooth, hyaline, granular, obliquely apiculate, 5–6 × 3–4μ; cystidia none; stipe viscid, smooth, glabrous, tapering downward, red, not soon fading, 1.5–2.5 × 0.1–0.2 cm.

Type collected by W. A. Murrill on low ground under hardwoods in Sugarfoot Hammock, near Gainesville, Fla., Nov. 7, 1938 (*F 18392*). The short stem and small spores separate it from near relatives. Found in abundance at one place. On drying the caps regain some of their lost color, becoming testaceous, while the stems remain red.

Clitocybe subeccentrica sp. nov.

Pileo convexo-umbilicato, 1.5–2.5 cm. lato, albo, glabro; lamellis confertis, sporis 6 × 4μ; stipite eccentrico, albo, 1.2–1.7 × 0.1–0.2 cm.

Pileus subcircular, convex to expanded, umbilicate, gregarious to cespitose, 1.5–2.5 cm. broad; surface dry, smooth, glabrous, uniformly white, unchanging, margin incurved, even, entire to undulate; context thin, white, odorless, fleshy, not reviving; lamellae decurrent, inserted, narrow, crowded, entire, yellowish or pale-rosy-isabelline; spores pip-shaped, smooth, hyaline, about 6 × 4μ; sterile cells few, subcylindric, smooth, hyaline, about 15 × 7μ; stipe equal, eccentric, smooth, subglabrous, white, whitish-mycelioid at the base, 1.2–1.7 × 0.1–0.2 cm.

Type collected by West, Arnold & Murrill on dead hardwood in Beech Woods, near Santa Fé, Fla., July 13, 1938 (*F 18385*). Suggesting *C. eccentrica* Peck but with different spores.

Prunulus subepipterygius sp. nov.

Pileo convexo-depresso, 1–2 cm. lato, viscido, sulcato; sporis ellipsoideis, 5–6 × 3–4μ; cystidiis subcylindricis, 15–30 × 15μ; stipite albo, glabro, 1–3 × 0.1–0.2 cm.

Pileus convex to plane, depressed at the center, gregarious to cespitose, 1–2 cm. broad; surface slimy-viscid, smooth, glabrous, sulcate, white, um-

brinous on the disk; context membranous, white; lamellae adnexed, narrow, tapering behind, medium distant, inserted, entire, white, unchanging; spores ellipsoid, smooth, hyaline, 1–guttulate, 5–6 $\times$ 3–4μ; cystidia subcylindric, smooth, hyaline, projecting 15–30 $\times$ 15μ, occupying the entire edge of the gill; stipe smooth, white, glabrous, viscid, ridged at the apex, 1–3 $\times$ 0.1– 0.2 cm.

Type collected by West and Murrill on a hardwood log in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 20, 1938 (*F 18363*). Also collected at the same place by West, Arnold and Murrill on an oak log, July 21, 1938 (*F 17910*). Evidently near *P. epipterygius* (Scop.) Murrill but having a shorter stem and smaller spores.

Prunulus syringescens sp. nov.

Pileo convexo, 1 cm. lato, subavellaneo; lamellis sinuatis, latis, sporis ovoideis, 5 $\times$ 3μ; stipite albo, glabro, 2.5 $\times$ 0.1 cm.

Pileus convex, not expanding, solitary, 1 cm. broad; surface dry, smooth, glabrous, opaque, pale-avellaneous, margin even, entire; context membranous; lamellae sinuate with decurrent tooth, broad, inserted, distant, pallid, toothed; spores ovoid, smooth, hyaline, 1–guttulate, about 5 $\times$ 3μ; cystidia none; stipe equal, smooth, glabrous, shining, white, 2.5 cm. long, scarcely 1 mm. thick. The entire hymenophore changes to pale-lilac on drying.

Type collected by W. A. Murrill on the ground in mixed woods just east of Gainesville, Fla., Oct. 29, 1938 (*F 18379*). A rare species, springing a surprise by its entire change of color.

Prunulus taxodii sp. nov.

Pileo conico-convexo, caespitoso, 1–1.5 cm. lato, nigro ad umbrino, sulcato; sporis 4–6 $\times$ 3–4μ, stipite subconcolori, 3 $\times$ 0.1 cm.

Pileus conic to broadly convex, often slightly umbilicate or truncate, cespitose or closely gregarious, 1–1.5 cm. broad; surface glabrous, black when young, umbrinous or fumosous in the older stages, distinctly sulcate-striate to the small central disk, which is very rugose; margin straight, entire, paler; context very thin, blackish, mild, odorless; lamellae adnate, broad, ventricose, inserted, distant, interveined, entire, cinereous, blackish near the context, blackening when bruised but not bleeding; spores irregular, subglobose to ellipsoid, smooth, hyaline, granular, 4–6 $\times$ 3–4μ; stipe equal, smooth, glabrous, whitish-shaggy at the base, blackish to avellaneous, not bleeding, about 3 $\times$ 0.1 cm.

Type collected by W. A. Murrill on the base of dead standing trunks of pond cypress in a cypress bog near Orange Heights, Alachua Co., Fla.,

Nov. 9, 1938 (*F 18376*). The trees were killed by a grass fire during a drought. So far as I now remember these are the first specimens of *Mycena* to be reported on *Taxodium* in America. Their color is quite peculiar; while the fresh spores suggest dried English peas.

Geopetalum viticola sp. nov.

Pileo semiresupinato, 3–7 mm. lato, striato, pallido; lamellis adnatis, praelatis, sporis ellipsoideis, 5–6 $\times$ 4μ.

Pileus broadly sessile, semiresupinate, closely gregarious, the reflexed portion thin, dimidiate, projecting 2–4 mm. and 3–7 mm. broad; surface glabrous, white-tomentose behind, distinctly striate over the gills, opaque-white, margin entire to rimose; context membranous, white, fleshy, fragile when dry; lamellae adnate, very broad, distant, inserted, pallid, edges uneven at times; spores broadly ellipsoid, apiculate, smooth, hyaline, 5–6 $\times$ 4μ; cystidia none.

Type collected by West and Murrill on a dead grape-vine near the ground at Arredonda, Fla., July 29, 1938 (*F 18317*). Dozens of hymenophores were examined, in all stages of development, but not one was found entirely resupinate nor was there a trace of a stipe in the entire lot.

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made:

> *Coltricia Mowryana* $=$ **Polystictus Mowryanus**
> *Galerula alachuana* $=$ **Galera alachuana**
> *Geopetalum viticola* $=$ **Pleurotus viticola**
> *Gymnopilus subdryophilus* $=$ **Flammula subdryophila**
> *Hydrocybe subminutula* $=$ **Hygrophorus subminutulus**
> *Prunulus subepipterygius* $=$ **Mycena subepipterygia**
> *Prunulus syringescens* $=$ **Mycena syringescens**
> *Prunulus taxodii* $=$ **Mycena taxodii**

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Buried Viable Seeds in a Successional Series of Old Field and Forest Soils

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(WITH TWO FIGURES)

INTRODUCTION

That seeds may germinate after prolonged burial under natural conditions has long been known. Salter (1857) reported a remarkable flora that appeared on mud upturned in the deepening of Poole Harbor, England. Similar instances were discussed by Becquerel (1907) in his review of odd floras observed on soil from excavations such as canals, wells, and race tracks. Shull (1914) described an exposed pond-bed which produced abundant vegetation.

Undoubtedly these reports and other similar observations led to the experimental burial of seeds by Duvel (1902, 1905) and Beal (1905). Duvel believed he had demonstrated that viability increases with depth of burial although Goss (1924), after study of the data of the same experiment, maintained that depth of burial affected vitality of the seeds but little. In 1930, Darlington (1931) reported that the seeds of four species buried by Beal in 1879 were still viable, indicating that some seeds may remain viable for 50 years when buried under proper conditions. The history of our knowledge of life-span of seeds has been adequately reviewed by Crocker (1938).

During the past 25 years there have been several investigations of naturally buried seeds in relation to above-ground vegetation. Brenchley and Adam (1915) estimated the seed content of arable land, using natural germination in the field as an indication of the buried population. Later, taking soil samples from the field and observing germinations in the greenhouse, Brenchley (1918) found that the seed content of different soil levels varied with the past history of the land. Warington (1924) showed

that the type of manure used on land affected its weed flora and hence its buried seed population. More recently Brenchley and Warington (1933) concluded that crop, soil type, and method of cultivation may influence the species and abundance of buried weed seeds.

Systematic studies of buried seeds in the forest floor have not been made since the report of Peter (1893), who found that the seeds of woody species occurred in soils of old forest while soils of new forest contained seeds of species common to cultivated land.

This suggested the present study of a series of sites whose past history is known, and which, vegetationally, bear a successional relationship to each other. By sampling soils from stands of a complete successional series (pioneers to climax) something should be learned of the length of time that naturally buried seeds may lie in the soil and remain viable. At the same time, there might be correlations between these buried seeds and the ages of the stands, and there might even be some clues to the mechanics of plant succession within the series.

Stands of all ages are readily available in the vicinity of Durham, N. C., for it is common practice to abandon fields when they cease to produce profitable crops. After abandonment, a weed population appears which shows a definite succession. The dominance of *Leptilon canadense* (L.) Britton denotes a field that has been lying fallow one year, while asters (*A. dumosus* L. and *A. ericoides* L.) and ragweed (*Ambrosia artemisiifolia* L.) indicate that the field has not been under cultivation for two years. At least three years without cultivation may be inferred from the dominance of *Andropogon* (chiefly *A. virginicus* L.) in an old field. When seed trees are available the fields are soon invaded by pines (*P. taeda* L. or *P. echinata* Mill.) which frequently become dominant within ten years. About a century later many of the pines will have been replaced by oaks and hickories, which indicate the ultimate climax forest.

Since this successional series invariably develops on old fields in this section, the seeds of the dominant species at least must be widely and evenly distributed. Some of these seeds probably do not germinate and they must lie buried in the forest floor. It seems plausible, therefore, that some seeds produced in one community would be present in the soil when subsequent communities occupy the site. By sampling the soil of representative communities of a successional series and subjecting these samples to uniform conditions favorable for germination, the resulting seedlings should be evidence of buried viable seeds.

METHODS

In the month of November, 1937, soil samples were obtained from twenty sites located in the Durham Division of the Duke Forest. Ten

ages, determined by the time since abandonment, were included in the series. Each age was represented by two sites. The ages are typical of old field succession in the Piedmont, ranging from a field cultivated in 1937 through pine dominance to an oak-hickory forest. One pine stand (*P. echinata*) in each age class had been studied by Billings (1938). All stands were on Granville sandy loam or closely related soil types and none showed evidence of cutting or other serious disturbance. The following ages were sampled:

Dominant	*Years abandoned*
1. Cultivated in 1937	0
2. *Leptilon*	1
3. *Aster-Ambrosia*	2
4. *Andropogon*	5

	Age of dominants[1]
5. Pine	15
6. Pine	33
7. Pine	58
8. Pine	85
9. Pine	112
10. Oak-hickory	200 plus

Within each site and within each duplicate site, two rectangular sampling areas were chosen, as similar in slope, exposure and cover as could be found.[2] Each sampling area was 10 by 20 feet (paced). The areas were cross-marked with a cord at 2-foot intervals and the sampling points determined from Tippett's (1927) Random Sampling numbers. The soil sampler used was the outer case of one devised by Coile (1936) for obtaining undisturbed soil samples. This is a steel cylinder 5.3 inches deep and 3.7 inches in diameter, with a volume of about 57 cubic inches. To insure the same depth and volume of soil for each sample, the coarse leafy litter, down to the fermentation layer, was removed from the sampling points on the forest floor. Precautions were taken to prevent contamination by seeds from sources other than the samples. Twenty samples were taken from each sampling area and dumped together upon an oilcloth. The pile was thoroughly mixed and then quartered. From a randomly selected quarter, a volume of soil equal to four sample portions (228 cubic

[1] The fields dominated by pine were probably abandoned from five to ten years longer than the ages indicated for the trees. It is doubtful if the hardwood sites were ever cultivated, for the stands were very uneven-aged with many trees over 200 years old.

[2] We acknowledge with thanks the assistance of Professor F. X. Schumacher of the Duke School of Forestry who gave invaluable advice on sampling methods and statistical treatment of the data.

inches) was taken as a composite sample. Since sampling areas were dupli-
cated in each site and two sites were sampled for each age class, the latter
were each represented by four composite samples. These were bagged and
stored at a temperature just above freezing until all samples were obtained.

All the soils were removed from the cold room on December 3 and each
composite sample was placed in a wooden flat on the earthen floor of the
greenhouse. To insure that no samples consciously received undue atten-
tion, the flats were filled and placed in the greenhouse in the order that the
mixture of bags was removed from storage. The soils were kept moist by
watering regularly. Since the samples, when spread in the flats, were
only about an inch deep, some tended to dry out very rapidly. A thin
mulch of powdered, sterilized sphagnum reduced evaporation. Two simi-
larly mulched flats of sterilized soil were placed with the samples as a check
on contamination by wind-borne seeds.

The first seedlings were removed on February 3, 1938, and as often
thereafter as individuals matured to an identifiable condition they were
removed. Competition was kept at a minimum by removing all but a few
of the individuals of any species which was particularly abundant. Those
remaining were permitted to flower and thus served to check identifications
based on purely vegetative characters.

Several species, germinating early in the experiment, tended to flower
at remarkably early stages in their development. These plants had scarcely
made any vegetative growth and had the appearance of dwarfed alpine
or arctic species. The phenomenon was probably a photoperiodic response
to the short days of the winter and spring months. Later it was found that
growth and consequently identification were facilitated by occasionally
sprinkling the flats with a dilute solution of a standard commercial
fertilizer.

RESULTS

Between February 3 and October 2, 1938, the germinations which
resulted in the flats yielded 5,989 plants. All these plants were considered
to be the product of seeds present in the soils when they were obtained from
the several sites, for no seedlings appeared in the check flats. Germina-
tions had apparently ceased when the last plants were removed in October.
The numbers and distribution of plants for the duplicate sites of each
age class are given in table 1. Unidentified seedlings, which numbered 125,
are not included. Most of these did not mature sufficiently to develop recog-
nizable characters.

The data are such that to discuss them it seemed desirable to know
whether, for certain species, the germinations occurred in sufficient num-
bers, or were so distributed, that they could not reasonably be ascribed

to chance. Accordingly the numbers of germinations for each of the 127 species were treated according to the method of analysis of variance of Fisher (Snedecor, 1937). When, in table 1 or in the discussion, a species is termed significant its germinations proved to have significant differences between age classes when subjected to the F test of Snedecor's table 10.2. Similarly it was determined which of the species within the wooded areas showed significant differences between pineland and hardwood. A further comparison was made within the areas that were not wooded. Here the germinations from the *Andropogon* sites were compared with the most recently abandoned fields. This division for comparison was chosen because the *Andropogon* field represents the best development of an herbaceous community before the dominance of upland fields by pine. Since forested areas represent something quite apart from land recently under cultivation, analyses were made to determine species significant in a comparison between the open and forested areas.

TABLE 1

List of Species and Numbers of Germinations in Soils from Duplicate Sites of Successive Age Classes

SPECIES APPEARING IN CULTIVATED FIELDS	AGES OF SITES										SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Allium spp.	19	3	18	10	0	..	..	..	..	..	x	x	..	..
	5	4	33	14	1	..	..	..	..	..				
Alopecurus carolinianus Walt.	14	..	..	..	..	..	..	..	..	..	..	..	..	..
	0	..	..	..	..	..	..	..	..	..				
Andropogon spp.	1	1	0	26	3	..	2	1	1	7	x	x	x	x
	4	1	1	33	0	..	1	0	2	1				
Barbarea verna (Mill.) Asch.	2	..	2	..	..	..	..	..	..	..	..	x	..	..
	0	..	0	..	..	..	..	..	..	..				
Cerastium viscosum L.	0	1	1	1	..	0	..	..	..	..	..	..	x	..
	1	0	0	5	..	1	..	..	..	..				
Cerastium vulgatum L.	0	..	..	1	..	..	..	..	..	..	..	x	..	..
	5	..	..	2	..	..	..	..	..	..				
Cyperus compressus L.	84	39	0	22	2	0	..	..	..	..	..	x	x	..
	34	154	18	0	15	3	..	..	..	..				
Cyperus flavescens L.	88	45	0	9	40	0	..	0	1	..	..	x	..	..
	60	427	13	2	62	1	..	2	0	..				
Digitaria sanguinalis (L.) Scop.	92	189	20	61	..	..	..	0	..	..	x	x	x	..
	66	142	49	17	..	..	..	3	..	..				

TABLE 1—*Continued*

| | AGES OF SITES | | | | | | | | | | SIGNIFICANT FOR: | | | |
	0	1	2	5	15	33	58	85	112	OII	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Erigeron and Aster spp.	1	8	1	1	3	0	2	0	1	2	..	x	..	.·.
	0	30	0	3	0	1	1	4	6	0				
Evonymus americanus L.	0	1	..	..	..	..	..	..	..	..	x	x	x	..
	1	2	..	..	..	..	..	..	..	..				
Fimbristylis autumnalis (L.) R. & S.	9	..	..	1	..	..	..	..	..	..	x	x	x	..
	6	..	..	0	..	..	..	..	..	..				
Fimbristylis laxa Vahl	24	..	0	..	0	..	..	..	..	..	..	x	..	..
	6	..	1	..	1	..	..	..	..	..				
Gnaphalium purpureum L.	5	2	0	3	29	1	8	3	4	6	..	..	..	..
	0	34	1	6	8	4	0	3	3	7				
Houstonia spp.	0	..	1	..	..	..	2	148	31	31	..	x	..	..
	5	..	1	..	..	..	1	0	15	0				
Holosteum umbellatum L.	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	0	..	..	..	..	..	..	..	..	..				
Juncus effusus L.	3	0	..	..	..	..	..	..	..	..	x	x	x	..
	1	1	..	..	..	..	..	..	..	..				
Krigia virginica (L.) Willd	11	..	..	2	..	0	-0	..	..	..	x	x	x	..
	15	..	..	3	..	1	1	..	..	..				
Linaria canadensis (L.) Dumont	8	10	0	0	19	3	3	1	..	..	x	x	x	x
	1	21	3	6	4	2	2	0	..	..				
Leptilon canadense (L.) Britton	3	7	1	0	..	..	0	..	0	3	..	x	..	x
	0	23	0	1	..	..	1	..	4	8				
Mollugo verticillata L.	4	1	2	3	0	1	0	1	..	..	..	x	..	x
	5	4	0	2	1	7	2	1	..	..				
Myosotis virginica (L.) BSP.	0	..	..	..	..	..	..	..	..	0	..	x	..	..
	3	..	..	..	..	..	..	..	..	1				
Oenothera laciniata Hill	1	2	2	0	5	..	..	..	..	..	..	x	..	..
	1	1	1	4	1	..	..	..	..	..				
Oxalis corniculata L.	4	0	2	4	..	..	5	1	9	5	..	x	..	x
	0	1	1	1	..	..	0	3	0	4				
Oxalis florida Salisb.	2	..	..	..	0	1	..	0	5	3	x	x	..	..
	0	..	..	..	2	0	..	2	5	0				
Oxalis stricta L.	14	1	5	2	0	0	4	0	2	0	..	x	..	..
	1	8	3	4	6	5	7	2	0	4				
Physalis virginiana Mill.	2	..	..	..	..	..	..	..	..	1	..	x	..	x
	0	..	..	..	..	..	..	..	..	0				

TABLE 1—*Continued*

	†				AGES OF SITES						SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Plantago virginica L.	9	..	20	19	4	..	..	..	1	..	..	x	x	..
	1	..	0	67	3	..	..	..	0	..				
Polygonum Persicaria L.	2	..	..	0	1	..	..	..	..	..	..	x	..	..
	0	..	..	1	0	..	..	..	..	..				
Polypremum procumbens L.	1	8	0	56	385	572	1	135	7	..	x	x	..	..
	3	1	13	1	27	221	6	58	3	..				
Sagina decumbens (Ell.) T. & G.	9	12	8	11	6	1	..	..	..	..	x	x	..	..
	30	1	11	20	3	0	..	..	..	..				
Scleranthus annuus L.	0	..	..	0	1	..	..	..	..	..	..	..	x	..
	4	..	..	1	0	..	..	..	..	..				
Specularia perfoliata (L.) A. DC.	2	2	10	4	10	..	1	1	..	..	..	x	x	..
	3	6	0	14	1	..	0	0	..	..				
Stenophyllus capillaris (L.) Britton	1	14	0	10	13	16	0	33	..	..	..	..	..	x
	5	0	2	5	6	4	1	24	..	..				
Sisymbrium thalianum (L.) J. Gay	0	23	9	0	..	..	..	1	..	..	x	x	x	..
	9	68	2	8	..	..	..	0	..	..				
Veronica peregrina L.	60	0	8	0	3	2	..	0	2	0	..	x	..	..
	3	30	0	27	5	1	..	1	0	1				

SPECIES ADDED BY THE ONE-YEAR FIELDS

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Chenopodium ambrosioides L.	..	0	..	..	..	..	..	..	..	..	..	..	x	..
	..	2	..	..	..	..	..	..	..	..				
Cyperus sabulosus Mart. & Schrad.	..	2	..	..	..	..	..	..	..	..	..	..	x	..
	..	0	..	..	..	..	..	..	..	..				
Dactyloctenium aegyptium (L.) Richter	..	0	..	..	..	..	..	..	..	..	..	..	..	..
	..	1	..	..	..	..	..	..	..	..				
Danthonia spicata (L.) Beauv.	..	0	..	..	..	..	..	2	..	..	..	..	..	..
	..	2	..	..	..	..	..	0	..	..				
Draba verna L.	..	6	..	..	..	..	..	..	..	..	..	..	x	..
	..	54	..	..	..	..	..	..	..	..				
Eleusine indica (L.) Gaertn.	..	1	..	..	..	..	..	..	..	..	..	..	..	..
	..	0	..	..	..	..	..	..	..	..				
Hieracium Gronovii L.	..	0	1	1	0	..	..	..	..	0	..	x	..	
	..	1	1	1	2	..	..	..	..	1				
Oenothera biennis L.	..	0	..	..	..	..	..	..	..	..	..	..	..	..
	..	1	..	..	..	..	..	..	..	..				

TABLE 1—*Continued*

					AGES OF SITES						SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Oxalis violacea L.	3	..	..	..	..	..	..	..		1	..	..	..	x
	..	0	..	..	..	..	..	..	..	3				
Solidago spp.	19	87	0	0	1	..	..	1	1	x	x	x	..
	..	14	78	5	12	1	..	..	12	0				
Trifolium arvense L.	0	..	7	..	..	..	..	..	..		..	..	x	..	..
	..	25	..	0	..	..	..	..	..	..				
Trifolium incarnatum L.	0	..	..	..	..	..	..	..	..		..	x	..	..
	..	3	..	..	..	..	..	..	..	..				
Xanthium cylindraceum	0	..	..	..	..	..	..	..	..		..	..	..	..
Millsp. & Sherff	..	1	..	..	..	..	..	..	..	..				

Amaranthus hybridus L.	..	1	..	..	..	..	..	..	..		..	..	..	..
	..	..	0	..	..	..	..	..	..	..				
Ambrosia artemisiifolia L.	..	1	0	1	1	..	..	..	..		..	x	..	..
	..	..	0	1	0	0	..	..	..	..				
Anthemis Cotula L.	..	0	0	1	0	..	..	0	0		..	x	..	x
	..	..	1	1	0	1	..	..	3	3				
Ascyrum hypericoides L.	..	0	2	1	..	0	..	1	..		x	x	x	..
	..	..	2	5	0	..	2	..	2	..				
Carara didyma (L.) Britton.. ..	..	0	..	..	..	..	..	..	..		..	..	..	..
	..	..	1	..	..	..	..	..	..	..				
Cyperus globulosus Aubl.	..	0	0	..	9	0	..	0	0		..	x	..	..
	..	..	1	3	..	0	2	..	2	1				
Diodia teres Walt.	..	1	..	..	..	..	..	..	..		..	x	..	..
	..	..	1	..	..	..	..	..	..	..				
Geranium carolinianum L.	..	2	..	..	..	..	..	..	..		..	x	..	..
	..	..	0	..	..	..	..	..	..	..				
Helenium tenuifolium Nutt... ..	..	2	..	..	..	..	..	..	..		..	x	..	..
	..	..	0	..	..	..	..	..	..	..				
Hypericum gentianoides (L.)	..	..	0	7	6	1	1	3	..	1	x	x	x	x
BSP.	..	..	3	15	7	3	0	0	..	0				
Hypericum mutilum L.	..	0	..	..	..	..	..	..	..		..	..	..	..
	..	..	1	..	..	..	..	..	..	..				
Lespedeza striata (Thunb.) ..	..	8	86	..	..	..	..	..	..		x	x	x	..
H. & A.	..	..	1	29	..	..	..	..	..	..				

TABLE 1—*Continued*

				AGES OF SITES							Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
	0	1	2	5	15	33	58	85	112	OH				
Plantago aristata Michx.	..	..	0	1	..	..	..	..	..	..		x	..	..
	..	..	1	0	..	..	..	..	..	..				
Plantago heterophylla Nutt...	..	..	0	..	..	..	..	..	..	..		x	..	..
	..	..	8	..	..	..	..	..	..	..				
Pyrrhopappus carolinianus ..	..	..	0	..	..	..	..	..	..	..		..	..	..
(Walt.) DC.	..	..	1	..	..	..	..	..	..	..				
Solanum carolinense L.	..	..	0	..	..	..	1	..	0	..		..	..	..
	..	..	1	..	..	..	0	..	1	..				
Specularia biflora (R. & P.)	..	..	4	0	..	..	..	..	..	..		x	..	..
F. & M.	..	..	0	1	..	..	..	..	..	..				
Veronica arvensis L.	..	..	3	0	..	..	..	1	..	..		x	x	..
	..	..	0	18	..	..	..	0	..	..				

SPECIES ADDED BY THE FIVE-YEAR FIELDS

Agrostis hyemalis (Walt.)...	..	..	..	0	..	..	..	..	0	..		x	x	..
BSP.	..	..	..	2	..	..	..	..	2	..				
Aristida spp.	..	..	..	6	0	..	..	..	..	..		x	x	..
	..	..	..	1	2	..	..	..	..	..				
Cassia nictitans L.	..	..	..	4	..	..	..	..	..	..	x	x	x	..
	..	..	..	13	..	..	..	..	..	..				
Eragrostis pilosa (L.) Beauv. ..	..	..	..	0	..	..	..	..	..	..		..	x	..
	..	..	..	1	..	..	..	..	..	..				
Euphorbia Preslii Guss.	..	..	..	0	..	..	..	..	..	..		..	x	..
	..	..	..	1	..	..	..	..	..	..				
Festuca octoflora Walt.	..	..	..	0	0 •	..	..	..	0	..		x	..	..
	..	..	..	2	1	..	..	..	7	..				
Festuca ovina L.	..	..	..	7	..	..	..	..	..	..	x	x	x	..
	..	..	..	2	..	..	..	..	..	..				
Poa annua L.	..	..	..	1	..	..	..	..	..	..		..	x	..
	..	..	..	0	..	..	..	..	..	..				
Poa cuspidata Nutt.	..	..	..	15	..	..	..	..	..	..		x	x	..
	..	..	..	0	..	..	..	..	..	..				

SPECIES ADDED BY THE FIFTEEN-YEAR SITES

Cyperus inflexus Muhl.	∴	..	..	..	0	..	..	..	..	..		x	..	..
	..	..	..	..	1	..	..	..	..	..				

TABLE 1—Continued

					AGES OF SITES						SIGNIFICANT FOR:			
	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Eragrostis spectabilis (Pursh.) Steud.					3	0		1		0		x		
					0	2		0		1				
Erechtites hieracifolia (L.) Raf.					1				1	1	x	x		x
					0				0	2				
Pagesia acuminata (Walt.) Pennell					0		1					x		x
					1		0							
Silene antirrhina L.					3							x		
					0									

SPECIES ADDED TO THE THIRTY-THREE-YEAR SITES

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Chrysopsis graminifolia (Michx.) Nutt.						0						x		
						2								
Eupatorium capillifolium (Lam.) Small						0						x		
						1								
Panicum dichotomum						5		2			x	x		x
						3		0						
Panicum sphaerocarpon Ell.						11	0	0	0			x		x
						3	1	1	3					
Panicum villosissimum Nash.						0	0	3	4	1		x		
						5	2	0	2	0				
Paspalum setaceum Michx.						1						x		
						0								
Potentilla pumila Poir						0	2			0		x		x
						1	0			3				
Trichostema dichotomum L.						0						x		
						1								
Viola sp.						0						x		
						1								

SPECIES ADDED BY THE FIFTY-EIGHT-YEAR SITES

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Broussonetia papyrifera (L.) Vent.							1					x		
							0							
Chrysopsis mariana (L.) Nutt.							0					x		
							1							
Cyperus strigosus L.							5			5		x		x
							0			0				

TABLE 1—*Continued*

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Gnaphalium obtusifolium L.	..	..	..	..	..	..	0	..	..	..	..	x	..	..
	..	..	..	..	..	..	1	..	..	..				
Panicum anceps Michx.	..	..	..	..	..	..	0	..	..	..	..	x	..	..
	..	..	..	..	..	..	1	..	..	..				
Panicum philadelphicum Bernh.	..	..	..	..	..	..	1	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				
Panicum xalapense HBK.	..	..	..	..	..	..	1	0	..	0	..	x	..	x
	..	..	..	..	..	..	0	1	..	3				
Rubus sp.	..	..	..	..	..	..	1	..	..	3	..	x	..	x
	..	..	..	..	..	..	0	..	..	0				
Sisyrinchium gramineum Curtis	..	..	..	..	..	..	1	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				
Verbascum Thapsus L.	..	..	..	..	..	..	2	..	..	..	..	x	..	..
	..	..	..	..	..	..	0	..	..	..				

SPECIES ADDED BY THE EIGHTY-FIVE-YEAR SITES

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Diodia virginiana L.	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Hypoxis hirsuta (L.) Coville	..	..	..	..	..	..	..	0	7	..				
	..	..	..	..	..	..	..	10	0	..				
Juncus scirpoides Lam.	..	..	..	..	..	..	..	14	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Oxydendrum arboreum (L.) DC.	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Panicum commutatum Schultes	..	..	..	..	..	..	..	1	..	..	..	x	..	..
	..	..	..	..	..	..	..	0	..	..				
Sambucus canadensis L.	..	..	..	..	..	..	..	0	..	..	..	x	..	..
	..	..	..	..	..	..	..	2	..	..				
Ulmus alata Michx.	..	..	..	..	..	..	..	0	..	..	..	x	..	..
	..	..	..	..	..	..	..	1	..	..				

SPECIES ADDED BY THE 112-YEAR SITES

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Agrostis alba L.	..	..	..	..	..	..	..	..	1	..	..	x	..	..
	..	..	..	..	..	..	..	..	0	..				
Cyperus cylindricus (Ell.) Britton	..	..	..	..	..	..	..	..	0	..	..	x	..	..
	..	..	..	..	..	..	..	..	1	..				

TABLE 1—*Concluded*

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Liquidambar styraciflua L.	..	..	..	..	..	..	..	..		1	..	x	..	..
	..	..	..	..	..	..	..	..		0	..			
Panicum lanuginosum Ell.	..	..	..	..	..	..	..	..		0	..	x	..	..
	..	..	..	..	..	..	..	..		1	..			
Prunella vulgaris L.	..	..	..	..	..	..	..	..	0	1	..	x	..	x
	..	..	..	..	..	..	..	..	1	0				
Rhus copallina L.	..	..	..	..	..	..	..	..		1	..	x	..	..
	..	..	..	..	..	..	..	..		0	..			
Scleria pauciflora Muhl.	..	..	..	..	..	..	..	..		0	..	x	..	..
	..	..	..	..	..	..	..	..		1	..			
Trifolium procumbens L.	..	..	..	..	..	..	..	..		0	..	x	..	..
	..	..	..	..	..	..	..	..		1	..			

SPECIES ADDED BY THE OAK-HICKORY SITES

	0	1	2	5	15	33	58	85	112	OH	Whole	Open vs. Forest	Early vs. Andropogon	Pine vs. Oak
Cercis canadensis L.	..	..	..	..	..	..	..	..		1	..	x	..	x
	..	..	..	..	..	..	..	..		0				
Eupatorium hyssopifolium L.	..	..	..	..	..	..	.:	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				
Galium pilosum Ait.	..	..	..	..	..	..	..	..		1	..	x	..	x
	..	..	..	..	..	..	..	..		0				
Hedeoma pulegioides (L.) Pers.	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				
Lactuca sp.	..	..	..	..	..	..	..	..		1	..	x	..	x
	..	..	..	..	..	..	..	..		0				
Morus rubra L.	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				
Panicum Ashei Pearson	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		2				
Panicum Boscii Poir.	..	..	..	..	..	..	..	..		1	x	x	..	x
	..	..	..	..	..	..	..	..		3				
Scutellaria sp.	..	..	..	..	..	..	..	..		1	..	x	..	x
	..	..	..	..	..	..	..	..		0				
Sonchus asper (L.) Hill	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				
Vaccinium sp.	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				
Viburnum affine Bush.	..	..	..	..	..	..	..	..		0	..	x	..	x
	..	..	..	..	..	..	..	..		1				

1. Origin of the germinating seeds

The majority of the germinations must have been derived from natu-rally buried seeds, for there was an average of 3.8 seedlings per square inch of natural surface sampled. Soils of fields abandoned one year yielded 1,463 germinations from samples with a field surface area totaling only slightly over one square foot (171.8 square inches) and a volume of about half a cubic foot. This, combined with the fact that over 90 per cent of the total germinations from each of the fields abandoned one, two, or five years were of species found growing in successionally younger fields, seems highly indicative of buried viable seeds.

It might be supposed that germinations in the forest soils resulted from seeds which were transported to the areas sampled, and that seeds from plants of an old-field community may effect an entrance into the interior of a pine stand. However, it seems improbable that many of the seeds could sift through the litter and fermentation zone, because of the thickness of these two layers after the stand is more than 20 years old. Billings (1938) charted the changes in the soil profile from an *Andropogon* field through the successional series of pine stands used in this investigation. The "plowed" horizon decreases, because it is becoming slowly incorporated in the A_2 horizon beneath it and the new A_1 horizon forming above it. The seeds buried in the plowed horizon are therefore incorporated in the A_1 and A_2 as the profile changes; they are not actually compacted in a layer of soil of decreasing width. Above the mineral soil there is a gradual accumulation of litter with the accompanying formation of the fermenta-tion layer. The litter layer increases from nothing in an old field to well over one and a half inches in the mature pine stands. The fermentation zone gradually reaches a depth of over half an inch in the mature stands. It is conceivable that, if the seeds were retained in this zone, conditions would be favorable for their germination in the damp mycelial mat of the fermentation layer soon after their entrance into the stand. After germina-tion, survival of the seedlings would depend upon their ability to com-pete with the new environmental condition. Any seeds germinating in the forest obviously could not be present to account for germinations in the flats. Those seeds of the old-field species which do germinate and survive in pine stands are limited in number (Billings) and decrease rapidly with each succeeding age class. Most of them probably do not reach the seed production stage before they die. Hence they are not responsible for the viable seeds in the forest floor.

The germinations of open-field species are undoubtedly products of seeds that were incorporated in the soil during cultivation or that entered

during the early years of abandonment. It is reasonable that these species
would contribute most since their seeds have not had to penetrate a litter
and fermentation layer in order to be mixed in the "plowed" horizon. Seeds
of characteristic forest species could not have been produced in the old
fields. Since they appeared only in the flats of forest soil, they must have
the ability to effect an entrance into the soil and their seedlings must be
so adapted that they survive where old-field species cannot.

It is doubtful that any germinations in the oak-hickory soils were
produced by seeds which lay buried in the soil since their formation in
some earlier successional community. All evidence indicates that the oak-
hickory sites have never been cultivated. Studies now in progress indicate
that several of these species, typical of the early stages in old-field suc-
cession, are practically eliminated as pine stands mature but that they may
again be characteristically present in the mature hardwood forest. Their
reappearance may be correlated with the opening of the stands as they
become over-mature and possibly with the changed leaf litter.

2. Distribution of numbers of germinations

Table 1 gives the number of germinations for the species as distributed
in the different age classes. Those species germinating in soils from the
greatest number of age classes are, without exception, species which appear
first (successionally) in the most recently abandoned field. Only *Gnapha-
lium purpureum* and *Polypremum procumbens* were represented in all age
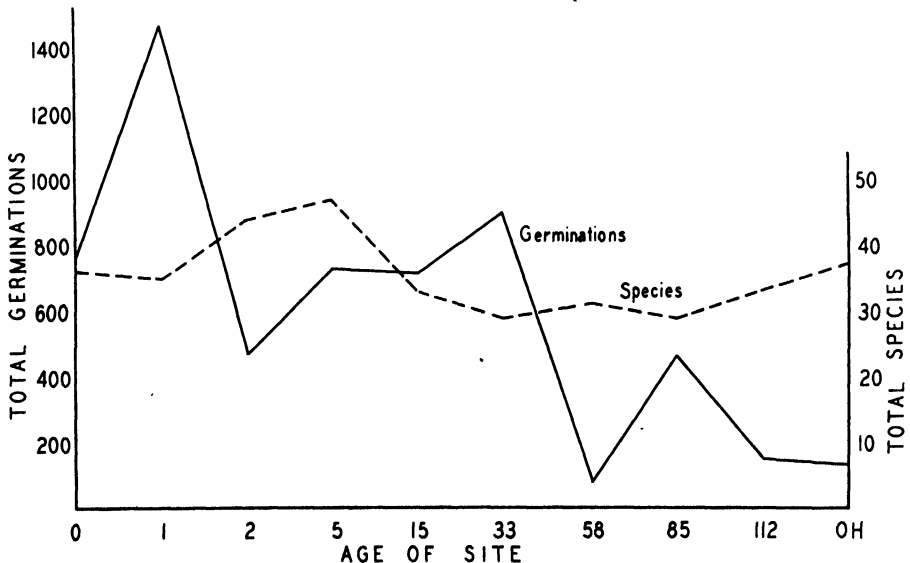
Fig. 1. Total germinations and total species that appeared in the soils from each
age class.

classes. The species of recently abandoned fields not only appeared in the greatest number of age classes but also made up the largest percentage of total species in each age class except oak-hickory. Every age class had "new species," meaning species which did not appear in soils from any lesser-aged stand.

Figure 1, in which all germinations are graphed, shows that the greatest number of germinations occurred in the soils of the 1-year fields while the greatest number of species appeared in soils from the 5-year fields. However, all that can be said of the total seed population should properly apply to the 21 species significant for the whole experiment. Their germinations are graphed in figure 2. The two peaks of germinations are here reversed, with the 33-year stand having by far the greatest number. This high value is the result of the excessive number of germinations of *Polypremum procumbens*, a significant species but, in other age classes, of much less importance. Of the significant species, the greatest number was again in the 5-year soils.
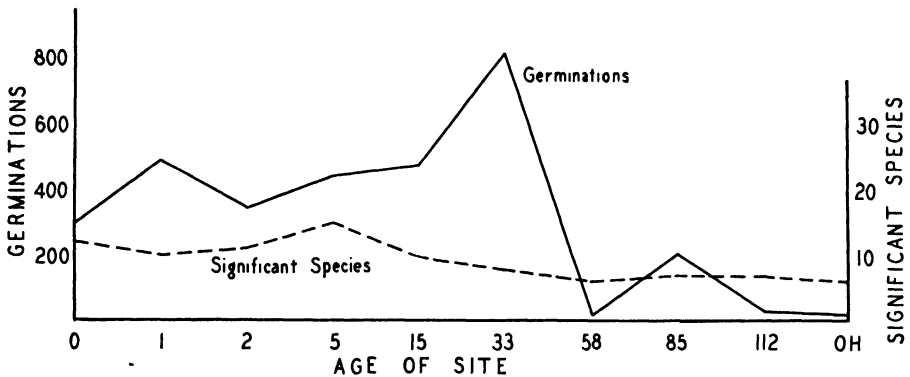
Fig. 2. Total significant species and their germinations for each age class.

Consideration of the distribution of significant species yields only a few generalizations. Those species producing sufficient germinations to be significant for the whole appeared first in open fields and younger pine stands. In spite of the numerous species and high germination counts for open fields, there were relatively few (25) species significant in the comparison between early fields and *Andropogon* dominance. Twelve of these species appeared in the cultivated field and eight did not come till *Andropogon* was dominant. The values serve to emphasize a correlation with the actual vegetation. Although many species are always present, only a few are dominant in size and numbers. The distinctness of the *Andropogon* field may be judged from its addition of nine species of which eight were significant in a comparison with earlier fields.

The comparison of open sites with wooded sites gives the most striking values for significant species. High percentages of the species added by each age of field were significant in this comparison, the cultivated field having 86 per cent. The consistent significance here is interpreted as an indication of the open-field nature of all these species. On the other hand, species appearing first in wooded stands were, without exception, all significant in the comparison. It cannot be entirely a matter of chance that those species which appear only in the soil from wooded stands should all then appear in significant numbers. Their seeds must not be transported elsewhere, or, as is more probable, must require the conditions of forest soil to retain viability.

The pine-hardwood comparison shows several early old-field species carrying over into pine stands in such numbers as to be significant. Those significant for pine were added in the young-to-middle-aged stands. The 85-year (mature) stand added no significant species and the over-mature (112-year) stand only one. Added species for the hardwood stand were, as before, all significant, these last added species being the portion of the viable seed population which is directly correlated with the dominants.

3. Relationships to Vegetation and Succession

The germinations of individual species become of special interest when considered in relation to their occurrence under natural conditions. All of the pine sites sampled in this study have been adequately described (Billings, 1938) on a phytosociological basis, and unpublished quadrat data (Oosting) are available for the oak-hickory stands and for herb stages of old-field succession. The general trend of old-field herbs begins with the abrupt appearance of large numbers of individuals which rarely maintain their importance for more than a year. The succeeding year finds the numbers materially reduced and thereafter there is a more or less gradual decline as trees become dominant. Many herbs of open old fields disappear entirely when trees appear, most are gone when the stand has attained middle age.

If the seeds of early old-field species are not especially viable, a natural break in the germination data should appear between the 5-year field and the 15-year pine. Also, if certain species germinate in soils from wooded stands in which, under natural conditions, Billings did not find them, these germinations should be excellent evidence of buried viable seeds, for the sampling is estimated at only 1 in 10,000.

The list of germinations includes 18 species of open-field herbs which appeared consistently for all age classes through 85 years or more. Of these species only three are recorded as growing naturally on the wooded sites and these only in the youngest stand. All are species which occur

consistently in old fields, usually with high frequencies and densities. Obviously they have been ,eliminated from membership in the forest community, although some are able to maintain themselves a few years longer than others. The general tendency for numbers of germinations to decrease with increased age class is apparent and is a strong argument for the existence of buried viable seeds, the viability decreasing with age. Reasoning on this basis, more evidence is available. Germinations of several open-field species are constantly present for all sites through the lesser age classes of pine. It might be concluded that seeds of these species had all germinated, or, what is more likely, that they were less viable and consequently died in the soil.

Certain inconsistencies in the distribution of numbers for individual species cannot be explained. *Polypremum procumbens* is a typical open-field herb and is not recorded as growing in pine forest, but it produced 412 seedlings in the 15-year age class and the remarkable number of 793 in the 33-year class. No other species approached these figures in total germinations. In contrast, the species of *Houstonia*, usually abundant in field and forest alike, produced no germinations in the 15- or 33-year soils although numerous in the soils from older stands.

In general, the counts for species that are statistically significant and are also listed in the quadrat records of the forested stands show no correlation with the above-ground vegetation. Of these species, only ten appear in the vegetation lists and many other species on the lists did not produce germinations in soil from any age class.

For herbaceous stands the numbers of germinations for an age class may sometimes be correlated with dominance in the previous age class and again may be an indication of what species will be important in the succeeding class. If, regardless of significance, the herb field species with highest germinations are considered by age classes, certain relationships to the field vegetation become apparent. The dominant weed species on a cultivated field at the end of the growing season is *Digitaria sanguinalis*. After a year of abandonment *Digitaria* is even more abundant and *Leptilon canadense* forms an open over-story three feet tall or more. A field abandoned two years is usually characterized by *Aster ericoides* or *Ambrosia artemisiifolia* or both. Thereafter a mixture of species is possible with *Andropogon* rapidly gaining dominance so that by the fourth year it is usually the most important species.

The species with high germinations are all regularly found in the old fields, although some have only seasonal importance. The species of *Sagina*, *Krigia*, *Sisymbrium*, and *Draba* are small in stature and abundant only vernally. Others appear only locally or are dwarfed by the larger and more conspicuous dominants.

The high germinations for *Digitaria* and the trend in numbers cor-
relate well with the distribution under field conditions. It is surprising
that the field just cultivated yielded no *Leptilon* seedlings for, under
normal conditions, it would surely have supported a goodly number of
individuals the next year if left fallow. The number of *Leptilon* germina-
tions for the 1-year field is related to the number of plants growing
there and indicates their probable presence in the field the next year.
Actually, 2-year fields have numerous *Leptilon* plants but they are
invariably dwarfed and depauperate. Indications are that by the third
year most of the seeds will have germinated, and probably the dwarfed
plants produce few seeds, so that *Leptilon* is soon eliminated from· the
old-field flora. The germination evidence supports these observations.

Germinations from 2-year fields are remarkably unrelated to above-
ground observations. Normally *Aster ericoides* and *Ambrosia* are the
dominants, as they were on the fields sampled. Peculiarly, not more than
one germination of *Ambrosia* was recorded for any age class. Difficulties
with identifications made it necessary to lump all germination counts of
Aster and *Erigeron*, but the combined value may be used as indicative of
Aster importance. Evidently the *Aster* germinations from the 1-year
field are indicators of the *Aster* dominance to come in the next year.
Although *Aster* was a dominant on the 2-year field only one germina-
tion occurred in the samples. There must have been many more seeds
present. Since the samples were collected in the fall and, except for the
brief storage in the cold room, thereafter never exposed to winter tem-
peratures, it is possible that the seeds require an after-ripening period.
This deficiency may also have contributed to the lack of germinations
of *Ambrosia* (*A. trifida* L. requires after-ripening; Davis, 1929) and
possibly other species as well.

The 5-year field had a good stand of *Andropogon virginicus*, char-
acteristic for the age class. The clumps were uniformly distributed and
spaced from about 6 inches to 2 feet apart. The appearance was that
of a pure stand with complete dominance. However, between the clumps
were numerous undersized plants of several species, almost all of which
had been present on younger fields. The germination lists indicate that
little or no *Andropogon* would have appeared on the 2-year field dur-
ing its third year of abandonment. This conforms with field conditions,
for the major appearance of *Andropogon* is apt to be in the fourth year.
Germinations in the 5-year samples indicate a potential increase in the
Andropogon population although actually it had probably about reached
its maximum.

Many species present in abundance in the early fields produced no
germinations in the wooded stands. This may be an indication that the

seeds of these species cannot retain their vitality for a long period of years. Evidence to support this idea is the fairly sharp decrease in the number of seeds germinating in soils from the 15-year pine as compared to the 5-year field. *Allium* drops from 24 to 5; *Digitaria* from 78 to 0; *Plantago virginica* from 86 to 7; *Cassia* from 17 to 0; *Lespedeza* from 115 to 0; and *Veronica peregrina* from 27 to 8. All of these species are statistically significant in the comparison between open and forested sites. To be sure, this radical decrease in germination may have been the result of germinations occurring naturally in the period between the field and the 15-year pine and not a loss of viability. These data are insufficient to prove either point.

Of the nine species added to the germination lists by the 5-year field seven were grasses. Numbers of germinations were not high and were rather in proportion to the importance of the species in this grass stage of old field succession. They represent an ephemeral condition which, with *Andropogon*, gradually disappears when trees become dominant. Billings (l. c.) found a few plants of *Andropogon* and *Eragrostis pilosa* in the 15-year pine stand, but *Andropogon*, *Aristida* and *Festuca octoflora* were the only species to produce germinations for this age class and they yielded only 3, 2 and 1, respectively.

Age classes beyond the establishment of pine show little correlation between natural vegetation and germinations. Numbers of herbs in pine forests are very small compared to those in open fields. With the relatively small soil samples used it is perhaps unwise to draw any conclusions. It is certain that, under natural conditions, field herbs decrease abruptly in total numbers and species with the development of pine. In a young stand of pine most of the old field herbs are eliminated and by middle age only scattered individuals remain, if any at all. At the same time new species of forest herbs have appeared, gradually increasing in abundance though never approaching open field numbers. The germination records show that viable seeds in the soil of these stands tend to include more and more species of wooded areas as the stands mature. However, the numbers never approach the concentrations of open fields.

When a forest stand becomes mature or over-mature, disturbances such as falling trees, etc., are not uncommon. If such a disturbance opens the crown cover and disturbs the accumulated litter there will immediately appear a crop of herbaceous species not at all related to the surrounding forest stand. These are the same species which, although characteristic of herb field succession, may appear sporadically in the forest quadrat records with very low densities and frequencies. They are likewise the same species which, producing tremendous numbers of germinations in open field soils, dropped off abruptly in soils where pine became dominant

but showed scattered germinations for age classes up to 112 years. Both the irregular appearances in undisturbed stands and the mass appearance in disturbed areas may reasonably be interpreted as resulting from buried viable seeds, for the presence of these seeds is here demonstrated by germination records.

It is disappointing to find no seedlings of the woody dominants in the soil from the forested sites. Sixteen species of woody seedlings were recorded with five of the species occurring in the oak-hickory site.

SUMMARY AND CONCLUSIONS

1. It is known that buried seeds may remain viable for long periods and studies have been made of naturally buried seeds as related to the vegetation.

2. To determine possible relations between buried seeds and past and future vegetation, soil samples were taken from a series of abandoned fields of known age and vegetative composition: a field under cultivation that season; fields fallow for 1, 2, and 5 years; shortleaf pine stands of 15, 33, 58, 85 and 112 years of age; and an oak-hickory forest. All stands had previously been studied phytosociologically and it is known that the series is representative of old field succession in the area.

3. Exposed to greenhouse conditions for 37 weeks the samples produced 5,989 seedlings. The seedlings represented 127 species of which 16 were woody ones.

4. The highest total germinations were produced by soil from the field which had been abandoned but one year. The 5-year field produced the greatest number of species.

5. The germination of seeds of several species in soil from habitats in which the parent plants do not grow indicates the possibility that, under natural conditions, seeds may lie buried for long periods and retain their viability.

6. Probably some seeds do not retain their viability under natural conditions, for several species which were very numerous in the stands of one age class produced few or no germinations in soil samples from the next succeeding class.

7. Statistical analyses of the occurrences of each of the species were made to ascertain which were significant throughout the series; in comparisons between open and forest; between the 5-year field and the preceding fields; and between pine and hardwood. The distribution of significant species serves to emphasize a relationship between vegetation and buried seeds; the distinctness of *Andropogon* fields; a difference between field and forest and between pine and hardwood; and that forest seeds apparently require forest conditions to retain their viability.

8. The germinations demonstrate the presence of viable seeds in the soil of all age classes sampled, but age and origin of the seeds remain problematical. They show a succession of species, as do the plants above ground, and, in general, they are indicative of that same succession.

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Additions to Florida Fungi—V [1]

William A. Murrill

The pileate species of the Hydnaceae are not abundant in central Florida nor are they exceptionally difficult, but the resupinate forms are many and intricate. Among the former, *H. zonatum, H. repandum, H. adustum, H. ochraceum, H. pulcherrimum,* and *H. erinaceus* are quite common; while *H. velutinum, H. diabolus, H. flavum,* and *H. rawakense* are frequent, and *H. fennicum, H. albidum, H. cristatum,* and *H. reniforme* either rare or very rare. Some of our most prominent and familiar northern species, such as *H. imbricatum, H. laciniatum, H. septentrionale, H. floriforme,* and *H. amicum,* are missing altogether; but resupinate species, like *H. plumosum, H. fasciculare,* and *H. fragilissimum,* more than fill their places.

Connecting links between this family and the Polyporaceae, such as *Irpiciporus lacteus, I. mollis,* and *Hydnochaete olivacea,* are commonly met with in the hammocks. Only one *Hydnum* (*H. floridanum* Berk. & Cooke) has previously been described from the Gainesville region and its description is rather too brief to be convincing.

Sarcodon alachuanum Murrill, sp. nov. Pileo convexo-subdepresso, 4–9 cm. lato, isabellino, disco fulvo, sapore farinaceo; sporis 4–5μ, stipite ferrugineo, 2–3 × 1–1.5 cm.

Pileus mostly circular, obconic to nearly plane or slightly depressed, gregarious or subcespitose, 4–9 cm. broad; surface smooth or somewhat uneven to colliculose, finely and densely short-pubescent, white to isabelline, fulvous on the disk with age, light-blue on the growing margin, which is rather thick, even, sterile, and usually somewhat lobed; context thick, mostly tough or woody, zonate, dark-blue when cut, with strongly farinaceous odor and farinaceous, nutty taste; teeth reaching 5 mm. long, dense, mostly terete, tapering, rusty-orange when young and fresh, fuliginous when dried; spores mostly globose, brownish, echinulate or tuberculate, about 4–5μ; stipe short, irregular, ferruginous-orange, hard or spongy, like the context within, about 2–3 × 1–1.5 cm.

Type collected by W. A. Murrill on the ground in woods at Gainesville, Fla., September 7, 1932 (*F 8335*). Also collected by the author at Gainesville, usually under oaks, from July to late September (*F 8402, F 18419, F 18423, F 18435*). Suggesting *H. ferrugipes* Coker and *H. cyaneotinctum* Peck but plaintly distinct from both.

Steccherinum subrawakense Murrill, sp. nov. Pileo conchato, 3–6 cm. lato, albo, glabro, sulcato; sporis ellipsoideis, hyalinis, 2.5–3 × 1–1.5μ.

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[1] The numbers cited in this article refer to specimens permanently deposited in the herbarium of the Florida Agricultural Experiment Station, at Gainesville. One species from Virginia is included.

Pileus conchate, flabelliform to dimidiate, imbricate, 3–4 × 3–6 × 0.5–1 cm.; surface white, glabrous, sulcate, nodulose to colliculose; margin thin, sterile, even, entire to undulate or slightly lobed; context tough, white, odorless, 2–4 cm. thick, drying rigid and woody, white or isabelline; teeth firm and tough, white, unchanging, terete or flat, pointed, simple or divided at the tip, crowded, 2–10 mm. long, yellowish or grayish in dried specimens; spores ellipsoid, smooth, hyaline, 1-guttulate, about 2.5–3 × 1–1.5μ.

Type collected by E. West and W. A. Murrill on a hardwood log in South Planera Hammock, eleven miles northwest of Gainesville, Fla., October 26, 1938 (*F 18420*). Found only once. Easily distinguished from *S. Westii* Murrill and other relatives.

Steccherinum Westii Murrill, sp. nov. Pileo effuso-reflexo, imbricato, dimidiato, 2–6 cm. lato, zonato, subglabro, pallido ad cremeo; sporis subglobosis ad ellipsoideis, hyalinis, 2μ longis.

Pileus effused-reflexed, laterally connate, imbricate; reflexd portion dimidiate, convex to expanded, 1–2 × 2–6 × 0.2–0.4 cm; surface subglabrous, zonate, rosy-isabelline to cremeous; margin pruinose, white, entire or undulate, very thin, sterile, deflexed on drying; context membranous, white, unchanging, fragile when dry; teeth terete, small, sharp, crowded, white, unchanging, 2–3 mm. long, fragile, the tips concolorous; spores subglobose or broadly ellipsoid, smooth, hyaline, 1-guttulate, copious, about 2μ long.

Type collected by E. West and W. A. Murrill on an oak log at Newnan's Lake, Fla., July 30, 1938 (*F 18006*). Also collected by A. S. Rhoads on a hardwood log at Hawthorn, Fla., August 18, 1935 (*F 8421*). Resembling *S. rawakense*.

Hydnum virginianum Murrill, sp. nov. Pileo convexo-subdepresso, 8–12 cm. lato, glabro, castaneo, lobato, sapore grato; sporis globosis, praetuberculatis, hyalinis, 4–5.5μ; stipite 2–3 × 2.5 cm.

Pileus irregularly circular, thick, convex to somewhat depressed, gregarious, 8–12 cm. broad; surface glabrous, castaneous, margin incurved, undulate or lobed, thick, white; context thick, fleshy, with pleasant odor and sweet, nutty taste, white, unchanging; hymenium milk-white, brownish where bruised, wood-brown in dried specimens; teeth short, sharp, crowded; spores globose, hyaline under microscope, roughly tuberculate, about 4–5.5μ; stipe very short, white to concolorous or paler, about 2–3 × 2.5 cm.

Type collected by W. A. Murrill under pines at Lynchburg, Va., October 22, 1926 (*F 18608*). Although the author collected a large number of hydnums in the vicinity of Lynchburg, this one was found only once. He decided that it must be edible but, fortunately, resisted the temptation to make sure of it.

Scutiger subrubescens Murrill, sp. nov. Pileo convexo-plano, 6–9 cm. lato, subtestaceo, squamuloso, felleo; tubulis albis ad sulphureis vel rosaceis, parvulis; sporis ovoideis, 4–5 × 2.5–3μ; stipite 2–4 × 1–2 cm.

Pileus subcircular, thin, convex with umbo to plane or somewhat depressed, gregarious, 6–9 cm. broad; surface pale-testaceous at the center fading out to nearly white on the margin, dry, rather smooth, decorated with tufts of fibrillose squamules, erect, dark-colored and conspicuous on the disk but reduced to mere specks near the margin, which is even, straight, very thin, fertile, undulate to deeply lobed; context thin, fleshy-tough, rigid and friable when dry, white or faintly pinkish, soon becoming quite bitter, having the odor of burnt sugar after drying; hymenium even, decurrent, white to sulfur-colored, usually becoming bay when dried except at the margin, which becomes pink; tubes circular to slightly angular, very short, 4–5 to a mm., walls very thin, becoming lacerate; spores ovoid, smooth, hyaline, copious, 1-guttulate, 4–5 × 2.5–3μ; cystidia none; stipe subequal, uneven, central or eccentric, glabrous, often changing to reddish-brown when dried, 2–4 × 1–2 cm.

Type collected by E. West and W. A. Murrill on the ground under oaks at Gainesville, Fla., November 23, 1938 (*F 18411*). A very interesting species, related to *Polyporus fractipes, P. laeticolor, P. Whiteae,* and *P. confluens.* It grows in leaf-mold, unattached to roots or other buried wood. The hymenophores are neither cespitose nor multiplex, though often quite lobed and irregular. The tufts of fibrils are mostly erect, not imbricate, and give the disk a tomentose appearance when dried. The change in color is both surprising and confusing because it does not always happen, even in large specimens, but as a rule the mature tubes change when dried while the young ones remain white or become pink. The surface and flesh of the cap do not undergo this change but either retain their original color or fade slightly. As to the odor of burnt sugar, it developed only during the drying process in an electric oven but remained strong and distinct in the herbarium. Oxidation processes are complicated and may be left for the chemist to discuss.

Russula incarnaticeps Murrill, sp. nov. Pileo convexo-depresso, 6–9 cm. lato, incarnato, striato, sapore grato; lamellis adnatis, latis, sporis cremeis, 8–10 × 7–8μ; stipite albo, 5–6 × 1.5–2 cm.

Pileus convex to deeply depressed, solitary or gregarious, 6–9 cm. broad; surface slightly viscid, smooth, glabrous, incarnate, margin striate, peeling, entire; context thin, white, odorless, mild; lamellae adnate, broad, ventricose, overlapping, close, equal, many-forked at the base, entire, white to slightly yellowish; spores globose or subglobose, distinctly echinulate, granular, cremeous in mass, 8–10 × 7–8μ; sterile cells frequent, hyaline, inflated at the base and abruptly tapering; stipe subequal, smooth, glabrous, white, unchanging, 5–6 × 1.5–2 cm.

Type collected by E. West and W. A. Murrill under oaks in Sugar-foot Hammock, November 23, 1938 (*F 18429*). A fine-looking, large, cool-weather species with very little flesh, drying light and fragile. The sterile cells are shaped like ink-bottles containing short-handled pens.

Russula lividirosea Murrill, sp. nov. Pileo convexo-plano, 5 cm. lato, livido, glabro, sapore grato; lamellis adnatis, albis, sporis globosis, albis, 6–7μ; stipite roseo, 3–4 × 1–1.5 cm.

Pileus convex to plane, solitary, 5 cm. broad; surface smooth, glabrous, lividous, or partly lilacinous, margin entire, even or faintly striate with age; context white, unchanging, thin, odor agreeable, taste nutty and sweet; lamellae equal, many-forked at the base, adnate with a slight decurrent tooth, slightly ventricose but narrow, subcrowded, entire, white to stramineous; spores globose or subglobose, rarely broadly ellipsoid, spinulose, 1-guttulate, hyaline, 6–7μ long; cystidia abundant, lanceolate or fusiform, hyaline, 50–80 × 10–15μ; stipe tapering upward, smooth, glabrous, solid, roseous, white at the base, 3–4 × 1–1.5 cm.

Type collected by W. A. Murrill under an oak in Gainesville, Fla., November 25, 1938 (*F 18451*). Also collected by the author under an oak in Gainesville, January 13, 1938 (*F 15930*). At first sight suggesting one of the color-forms of *R. Mariae* Peck but not at all pruinose and, of course, quite different microscopically. It is a beautiful species even for *Russula*, with its livid cap and pink stem, and seems to be very rare, appearing only in winter. The cystidia are wondrous to behold, either when attached to the gills or when floating by the score among the spinulose spores.

Russula roseitincta Murrill, sp. nov. Pileo convexo-subdepresso, 6 cm. lato, glabro, sapore grato; lamellis adnatis, furcatis, sporis albis, 8–9 × 6–7μ; stipite albo ad subroseo, 5 × 1.2 cm.

Pileus convex to plane, slightly depressed at the center, solitary, 6 cm. broad; surface slightly viscid when moist, smooth, glabrous, rosy-avellaneous-isabelline, margin even, entire, peeling; context thin, white, odorless, mild; lamellae adnate, equal, medium broad, rather close, many-forked at the base, a few midway, entire, white, unchanging; spores white, mostly broadly ellipsoid, 1-guttulate, conspicuously and densely echinulate, 8–9 × 6–7μ; sterile cells few, hyaline, inflated, 20–30 × 15μ, with threadlike tips of varying lengths; stipe equal, smooth, glabrous, white, rose-tinted when dry, 5 × 1.2 cm.

Type collected by E. West and W. A. Murrill on the ground in mixed woods at Newnan's Lake, Fla., November 15, 1938 (*F 18453*). Near *R. rosei-isabellina* Murrill but with different microscopic characters and gill structure.

Russula subacris Murrill, sp. nov. Pileo convexo-subdepresso, 3–5 cm. lato, glabro, rubro, acrido; lamellis adnexis, confertis, albis; sporis ellipsoideis, echinulatis, albis, 10 × 7μ; stipite glabro, albo, 1.5–3 × 0.5–1.3 cm.

Pileus convex to slightly depressed, gregarious, 3–5 cm. broad; surface smooth, glabrous, slightly viscid, varying from dark-incarnate to pale-purple; margin entire, even, often becoming quite striate with age, peeling very readily; context thin, white, unchanging, odorless, only moderately acrid; lamellae adnexed, slightly sinuate, equal, close, narrow, entire, pure-white, unchanging; spores chalk-white in mass, broadly ellipsoid, distinctly but not strongly echinulate, about 10 × 7μ; cystidia few, flask-shaped, hyaline, about 35 × 10μ; stipe equal or subequal, smooth, glabrous, milk-white, 1.5–3 × 0.5–1.3 cm.

Type collected by West, Arnold and Murrill in moist ground under deciduous trees at Planera Hammock, eleven miles northwest of Gainesville, Fla., January 3, 1939 (*F 19508*). Also collected by Mr. J. R. Watson in low grassy ground at Myakka Lake, Sarasota Co., Fla., December 26, 1938 (*F 19227*). A small red species which peels very readily but is not nearly so acrid as *R. emetica*. It appears only in midwinter.

Russula subgranulosa Murrill, sp. nov. Pileo convexo-depresso, 8 cm. lato, avellaneo, sapore grato; lamellis subadnexis, non furcatis, sporis stramineis, ellipsoideis, 9–10 × 6–7μ; stipite albo, 5 × 1.5 cm.

Pileus convex to depressed, solitary, 8 cm. broad; surface dry, avellaneous with yellowish tints, lilac at the center, the cuticle breaking into small granules visible under a handlens, margin even, entire, not peeling; context thin, white, unchanging, odorless, mild; lamellae just touching the stipe by a tooth, rounded behind, medium broad and medium distant, slightly ventricose, equal, none forked anywhere, entire, white to pale-yellow; spores mostly broadly ellipsoid, 1-guttulate, conspicuously echinulate, stramineous in mass, about 9–10 × 6–7μ; cystidia none; stipe equal, smooth, glabrous, slightly granular at the apex, white, with a rosy tint in one place, 5 × 1.5 cm.

Type collected by E. West and W. A. Murrill on the ground in mixed woods at Newnan's Lake, Fla., November 15, 1938 (*F 18433*). Near *R. roseitincta* Murrill but the spores are pale-yellow and the gills are not forked anywhere, even at the very base.

Melanoleuca margarita Murrill, sp. nov. Pileo convexo, 1.5–2 cm. lato, albo, subfelleo; lamellis albis, sporis ovoideis, 3–4 × 1.5–2μ; stipite albo, subradicato, subclavato, 4–6 × 0.4–0.8 cm.

Pileus convex, not expanding, gregarious, 1.5–2 cm. broad; surface smooth, dry, finely fibrillose, pearly-white with a bluish tint, margin even, entire to undulate; context white, odorless, not acrid but becoming slightly bitter; lamellae sinuate, plane, close, medium broad, inserted, entire, white, unchanging; spores ovoid, smooth, hyaline, 1-guttulate, 3–4 × 1.5–2μ; cystidia none;

stipe above ground subequal, smooth, slightly fibrillose, solid, white, mostly fulvous when dried, 2–3 × 0.4–0.6 cm.; buried portion clavate, not definitely radicate, 2–3 × 0.8 cm.

Type collected by E. West and W. A. Murrill on low ground under hardwood trees near Hogtown Creek, Gainesville, Fla., November 23, 1938 (*F 18454*). Suggesting *M. acris* (Peck) Murrill but not acrid and having smaller, ovoid spores.

Galerula Westii Murrill, sp. nov. Pileo conico-subexpanso, umbonato, gregario, 1–1.5 cm. lato, fulvo ad isabellino; lamellis adnatis, latis, sporis ellipsoideis, 8 × 5μ; stipite albo, 3–4 × 0.2–0.3 cm.

Pileus conic to subexpanded, umbonate, closely gregarious, 1–1.5 cm. broad; surface hygrophanous, fulvous when moist, isabelline when dry, becoming fulvous again after artificial drying, smooth, pruinose, margin even, straight and appressed when young; context very thin, white, odorless, mild; lamellae adnate, broad, distant, inserted, entire, pallid to subferruginous; spores ellipsoid, smooth, 1-guttulate, pale-ferruginous, about 8 × 5μ; cystidia none; stipe cartilaginous, equal, smooth, glabrous, white, 3–4 × 0.2–0.3 cm.; veil slight, whitish, disappearing at a very early stage and leaving no annulus.

Type collected by E. West and W. A. Murrill in damp soil under hardwood trees in Sugarfoot Hammock, near Gainesville, Fla., November 23, 1938 (*F 18428*). Abundant in the type locality but not found elsewhere. The conic umbo is prominent and rather distinctive.

Naucoria cuspidata Murrill, sp. nov. Pileo campanulato-depresso, umbonato, 1.5–3 cm. lato, fulvo; lamellis emarginatis, sporis ellipsoideis, tuberculatis, 8–9 × 5μ; stipite isabellino, 4–5 × 0.3–0.4 cm.

Pileus campanulate to depressed with a small conic umbo, gregarious, 1.5–3 cm. broad; surface hygrophanous, smooth, finely innate-fibrillose, uniformly fulvous, margin even, entire to undulate; context very thin, without characteristic odor; lamellae emarginate, medium distant, plane but rather broad, inserted, very thin, fringed on the edges, becoming ferruginous or fulvous; spores ellipsoid, obliquely apiculate, granular, finely but distinctly tuberculate, ferruginous, about 8–9 × 5μ; cystidia none; stipe fleshy with a tough rind, subequal, striate, fibrillose, isabelline, 4–5 × 0.3–0.4 cm.

Type collected by E. West and W. À. Murrill on damp ground under hardwood trees in Sugarfoot Hammock, near Gainesville, Fla., November 23, 1938 (*F 18432*). Suggesting *N. praeumbonata* Murrill but differently colored and having tuberculate spores.

Gymnopilus armillatus Murrill, sp. nov. Pileo convexo-expanso, caespitoso, 5–10 cm. lato, glabro, ochroleuco, disco subluteo, praefelleo; lamellis sinuatis, confertis, sporis ellipsoideis vel ovoideis, 8–10 × 5–6μ; stipite striato, 10 × 1–1.5 cm., annulo amplo, persistente.

Pileus convex to expanded, cespitose, 5–10 cm. broad; surface smooth, not viscid, subglabrous to glabrous, ochroleucous, pale-luteous on the disk, margin even, entire; context thick at the center, pale-yellow, very bitter, odorless; lamellae broad, crowded, entire, sinuate with decurrent tooth, luteous-flavous, becoming fulvous with age; spores ovoid or ellipsoid, smooth, ferruginous 1-guttulate, 8–10 $\times$ 5–6μ; cystidia none; stipe equal, fleshy-tough, striate, fibrillose, pale-yellow at the apex, darker below, brownish or blackish at the base, about 10 $\times$ 1–1.5 cm.; annulus superior, ample, membranous, yellow, persistent.

Type collected by A. S. Rhoads on the root of a living sweet-gum tree, causing a whitish rot, at Bithlo, Orange Co., Fla., December 21, 1932 (*F 15731*). Cotype collected by J. R. Watson near oaks at Myakka Lake, Sarasota Co., Fla., December 26, 1938 (*F 19507*). A large, clustered species with a distinct ring; apparently confined to central Florida.

NEW COMBINATIONS

For the convenience of those who use Saccardo's nomenclature the following new combinations are made:

> *Galerula Westii* = **Galera Westii**
> *Gymnopilus armillatus* = **Flammula armillata**
> *Melanoleuca margarita* = **Tricholoma margarita**
> *Sarcodon alachuanum* = **Hydnum alachuanum**
> *Steccherinum subrawakense* = **Hydnum subrawakense**
> *Steccherinum Westii* = **Hydnum Westii**

HERBARIUM, FLORIDA AGRICULTURAL EXPERIMENT STATION
    GAINESVILLE, FLORIDA

A Collection of Flowering Plants from Mount Roraima and adjacent Venezuela, British Guiana, and Brazil

By A. C. Smith (and collaborators)

Between September, 1938, and February, 1939, Mr. Albert S. Pinkus made a trip from Georgetown to the vicinity of Mount Roraima, during which he assembled 290 numbers of herbarium specimens in several sets. This collection comes from a region of extreme botanical interest, which has been visited by several collectors, but which, upon being revisited, always discloses new or otherwise noteworthy species. Mr. Pinkus' route took him up the Mazaruni River in British Guiana to the Kurupung River, thence overland to the junction of the Mazaruni with the Kamarang River, which was ascended. Following the Pakaraima Mountains on the Venezuelan side, the collector reached Arabupu, the historic locality near the base of Mount Roraima. Three months were spent in this region, including ten days on the summit of Mount Roraima, which was ascended by means of the famous "Ledge." The return trip was made along the Pakaraima Range east of Mount Roraima to the head of the Kukui River, which was followed back to the Mazaruni region.

The few collections already made in the vicinity of Mount Roraima serve to emphasize the remarkable endemism of the flora. Perhaps the most interesting feature of Mr. Pinkus' work is the re-collection of some of the endemic species, many of which are represented by scanty material and which are better understood with every new visit to the region. Following is a list of species which were collected from essentially the type locality (summit or southwestern slopes of Mount Roraima, including the vicinity of Arabupu). Mr. Pinkus' collection number is indicated in italics following the name; in some cases the specimen represents the second collection of the species.

Nietneria corymbosa Kl. & Rich. Schomb., *107*.
Tofieldia Schomburgkiana Oliver, *290*.
Epidendrum alsum Ridley, *103*.
Epidendrum montigenum Ridley, *99*.
Octomeria Connellii Rolfe, *101*.
Pogonia parviflora (Lindl.) Reichb. f., *156*.
Sobralia stenophylla Lindl., *54*.
Roupala Schomburgkii Kl., *50*.
Ocotea roraimae Mez, *145*.
Weinmannia guyanensis Kl., *289*.
Weinmannia laxiramea Killip & Smith, *106*.
Licania rufescens Kl., *62*.
Ravenia ruellioides Oliver, *141*.

Qualea Schomburgkiana Warm., *64*.
Chaetocarpus stipularis Gleason, *56, 81*.
Cyrilla brevifolia N. E. Brown, *100, 155*.
Ilex retusa Kl., *120*.
Ouratea Tatei Gleason, *80*.
Poecilandra retusa Tul., *158*.
Sauvagesia Imthurniana (Oliver) Dwyer, *116*.
Archytaea multiflora Benth., *48*.
Bonnetia roraimae Oliver, *111*.
Myrtus roraimensis N. E. Brown, *102*.
Miconia rupestris Ule, *137*.
Miconia superba Ule, *66*.
Sciodaphyllum umbellatum N. E. Brown, *153*.

Befaria Tatei Gleason, *108.*

Ledothamnus sessiliflorus N. E. Brown, *104.*

Pernettya marginata N. E. Brown, *113, 114.*

Thibaudia formosa Kl., *128.*

Thibaudia nutans Kl., *39.*

Thibaudia Ulei (Mansf.) A. C. Smith, *105, 149.*

Bonyunia superba Rich. Schomb., *270.*

Calolisianthus Imthurnianus (Oliver) Gleason, *117.*

Symbolanthus Elisabethae (Schomb.) Gilg., *160.*

Cordia hirta Johnston, *69.*

Hyptis arborea Benth., *43.*

Orchyllium Campbellianum (Oliver) Gleason, *133.*

Orchyllium Humboldtii (Schomb.) Barnh., *151.*

Orchyllium Quelchii (N. E. Brown) Gleason, *118.*

Palicourea obtusata Krause, *126.*

Psychotria crassa Benth., *119.*

Psychotria oblita Wernh., *121, 148.*

Viburnum roraimense Killip & Smith, *138, 139.*

Baccharis Schomburgkii Baker, *125.*

Baccharis Vitis-idaea Oliver, *110.*

Calea Oliverii Robins. & Greenm., *76, 124.*

Eupatorium roupalifolium Robins., *159.*

Mikania pannosa Baker, *57.*

Quelchia conferta N. E. Brown, *112.*

Stenopadus condensatus (Baker) Blake, *157.*

Vernonia ehretifolia Benth., *123.*

In the remainder of this treatment several noteworthy species are discussed, fifteen which are apparently new are described, and two new combinations are made. In identifying the collection I have enjoyed the kind collaboration of several specialists, and I take this opportunity to express appreciation to Messrs. S. F. Blake, L. Croizat, J. D. Dwyer, H. A. Gleason, E. P. Killip, H. N. Moldenke, P. C. Standley, L. O. Williams, and R. E. Woodson. Some of these have kindly permitted their work to be included in the present paper. The first set of the collection, including types unless otherwise noted, is deposited in the herbarium of the New York Botanical Garden.

SMILACACEAE

Smilax immersa A. C. Smith, sp. nov. Frutex scandens ubique praeter perianthii segmentos apicem versus minute et obscure tomentellos glaber; ramulis teretibus minute tuberculatis inermis; petiolis crassis 2.5–3.5 cm. longis, marginibus inflexis 7–10 mm. longis extremitate obtusis vel subacutis vaginatis, apicem versus incrassatis et rugosis; laminis coriaceis opacis elliptico-oblongis, 10–19 cm. longis, 3.5–8 cm. latis, basi acutis vel attenuatis et in petiolum decurrentibus, apice breviter calloso-cuspidatis, margine anguste recurvatis, e basi 3-(vel obscure 5-) nerviis, nervis extimis inconspicuis, alteris supra valde impressis vel interdum planis subtus prominentibus, rete venularum subimmerso vel leviter prominulo; pedunculis umbellarum mascularum in racemis bracteatis ad 6 cm. longis dispositis vel raro solitariis; bracteis oblongis acutis 2–5 mm. longis; pedunculis 4–13 mm. longis paullo compressis; receptaculis masculis subglobosis circiter 2 mm. diametro, bracteolis oblongo-lanceolatis 0.5–1 mm. longis; floribus 15–30 per umbellam; pedicellis gracilibus 5–6 mm. longis; perianthii segmentis elliptico-lanceolatis, 3.5–4.5 mm.

longis, 1–1.2 mm. latis, acutis; filamentis membranaceis 1.5–2.2 mm. longis, antheris oblongis subacutis quam filamentis paullo brevioribus.

Type, *Pinkus 37*, collected October 3, 1938, along Membaru Creek, upper Mazaruni River region, British Guiana. *S. immersa* is characterized by its thick smooth elliptic leaf-blades with basal principal nerves and immersed veinlets, its unarmed stems, its inflorescences with several umbels, and its very slender pedicels. Its relationship appears to be with *S. Schomburgkiana* Kunth and *S. pseudosyphilitica* Kunth, species readily distinguished by their reticulate venation.

ORCHIDACEAE[1]

POGONIA PARVIFLORA (Lindl.) Reichb.f. Venezuela: southwestern slopes of Mount Roraima, alt. about 7200 ft., *Pinkus 156*; growing in swampy open places; perianth purple; stem and some leaves red. This collection, from the type locality, is of especial interest because the flowers are somewhat smaller than those previously known. Following is a description of the flowers based on *Pinkus 156*:

Sepals about 25 mm. long and 8 mm. broad, oblong-elliptic, acute, apiculate, about 7-nerved, navicular; petals about 22 mm. long and 10 mm. broad, oblong-obovate, obtuse or acutish, minutely denticulate, with about 7 principal nerves; lip about 22 mm. long and 13 mm. broad, obovate, entire or with a very small terminal lobe, the lamina with a fleshy bilamellate callus extending from the base to the apex, with two clavellate callous processes about 3 mm. long at the base of the lip, one on either side of the central callus; column about 18 mm. long, slightly arcuate; pollen simple, not in tetrads.

ROSACEAE[2]

Licania exiguifolia Standley, sp. nov. Arbor 10-metralis, trunco 15 cm. diam., ut videtur dense ramosa, ramulis gracilibus sed rigidis teretibus griseo-fuscis vel fusco-ferrugineis elevato-lenticellatis adpresso-pilosis vel strigosis, internodiis brevibus vel brevissimis; folia parva petiolata rigide coriacea, petiolo crassiusculo 4–5 mm. longo strigoso vel glabro; lamina oblongo-elliptica vel oblongo-ovata 3–5 cm. longa 1.5–2 cm. lata sensim vel subabrupte acuminata vel longe acuminata, basi acuta, supra in sicco fuscescens sub lucida glabra vel tantum ad costam valde impressam strigosa, nervis vix manifestis planis, subtus pallidior griseo-ochracea ubique densissime adpresso-tomentosa, ad costam nervosque adpresso-pilosa, costa crassiuscula elevata, nervis lateralibus utroque latere 7–8 prominentibus valde obliquis angulo semirecto adscendentibus marginem attingentibus, venis tomento fere omnino occultis; inflorescentia non visa; fructus depresso-globosus 2–2.5 cm. latus 1.7–2 cm.

[1] By L. O. Williams.
[2] By P. C. Standley.

altus, basi et apice latissime rotundatus lucidus brunneo-ferrugineus ubique dense pallido-lenticellatus.

Type, *Pinkus 245*, collected February 21, 1939, along trail between Membaru Creek and Makreba Falls on Kurupung River, upper Mazaruni region, British Guiana, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.).

Licania roraimensis Standley, sp. nov. Arbor 18-metralis, trunco 30 cm. diam., ramulis teretibus in sicco griseo-fuscis rimosis elevato-lenticellatis, internodiis brevibus, novellis non visis; folia mediocria breviter petiolata rigide coriacea, petiolo crasso 7–10 mm. longo supra late canaliculato glabro vel glabrato; lamina elliptica vel oblongo-elliptica 9.5–13 cm. longa 4.5–6 cm. lata sensim vel subito attenuato-acuminata, acumine angusto longe attenuato usque 2 cm. longo, basi plus minusve obliqua obtusa vel anguste rotundata, supra sublucida glabra, costa plana, nervis venisque non elevatis subtus pallidior ochracea, glabrata sed inter venulas adpresso-tomentulosa, costa crassiuscula elevata, nervis lateralibus utroque latere 5–6 obliquis angulo semirecto vel paullo latiore adscendentibus subarcuatis marginem fere attingentibus, venulis prominentibus atque incrassatis arctissime reticulatis, margine quoque valde incrassato atque cartilagineo; inflorescentia (cum floribus imperfectis et vetustis tantum visa) terminalis vel axillaris racemoso-paniculata sessilis 6–10 cm. longa pauciramosa, ramis crassiusculis dense et minute sordido-puberulis, floribus sessilibus vel breviter crasse pedicellatis; calyx 4 mm. longus dense et minute puberulo-tomentellus campanulatus, lobis erectis ovato-ovalibus obtusis vix 1.2 mm. longis; cetera ignota.

Type, *Pinkus 61*, collected December 15, 1938, in the vicinity of Arabupu, Mount Roraima District, alt. about 4200 ft., Venezuela, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.).

Licania pallidula Standley, sp. nov. Arbor 24-metralis, trunco 30 cm. diam., ramulis gracilibus teretibus ferrugineo-ochraceis rimosis elevato-lenticellatis, novellis ferrugineis glabris; folia mediocria brevissime petiolata coriacea rigida, petiolo crasso 3–5 mm. longo glabro; lamina elliptica, obovato-elliptica vel oblongo-obovata 7–9 cm. longa 3.5–5.5 cm. lata obtusa vel rarius anguste rotundata, basi acuta et subcontracta, supra plus minusve lucida in sicco pallide viridis glabra, costa prominente, nervis manifestis atque interdum prominulis, subtus glauco-viridis ubique costa nervisque exceptis tomento minutissimo pallido adpresso obtecta, costa prominente, nervis lateralibus utroque latere ca. 8 prominentibus tenerrimis angulo latiusculo adscendentibus remote a margine arcuato-conjunctis subarcuatis, venulis prominulis laxe reticulatis gracilibus; paniculae terminales atque axillares pauciramosae longe pedunculatae ca. 5 cm. longae, ramis rigidis adscendentibus ferrugineis sparse vel dense et minute

strigillosis, floribus (perfectis non visis) racemosis sessilibus vel brevissime et crasse pedicellatis; calyx persistens ca. 3 mm. longus dense minutissime ochraceo-tomentellus, dentibus rotundato-ovatis obtusis brevissimis erectis; fructus valde immaturus obovatus 7 mm. longus apice late rotundatus, basin versus sensim attenuatus, dense atque minutissime ochraceo-tomentellus.

Type, *Pinkus 89*, collected December 28, 1938, in second growth on clay soil, on southwestern slopes of Mount Roraima, vinicity of Arabupu, alt. about 4600 ft., Venezuela, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.). An apparently well marked species, notable for the very minute tomentum that gives a glaucous appearance to the lower leaf-surface. In this, as in the other species here described, the specimens are in fruit or very advanced anthesis, so that it is impossible to describe the floral details.

CAESALPINIACEAE

DIMORPHANDRA CONGESTIFLORA Sprague & Sandwith. British Guiana: near Makreba Falls, Kurupung River, upper Mazaruni region, *Pinkus 7*. Excellent flowering material of a rare species, from the type locality.

DIMORPHANDRA CUPREA Sprague & Sandwith. British Guiana: Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., *Pinkus 203*. Previously known from the vicinity of Kaieteur Savanna.

DICYMBE JENMANI Sandwith. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 31, 237*. Our material, compared with that previously known from Kaieteur Savanna, has the leaflets in two or three, rather than four, pairs, the veinlet reticulation somewhat more obvious on the upper leaf-surface, and the sepals uniformly sericeous without rather than sericeous only along a mid-line, but hardly appears to differ conspicuously. The collector notes the present specimens as trees 20 and 70 feet high. In the two flowers dissected there were 9 ovules in each ovary, 10 being mentioned in the original description.

FABACEAE

ALEXA IMPERATRICIS (Schomb.) Baker. British Guiana: upper Arubaru River (Kako tributary), Mazaruni drainage, alt. about 2000 ft., *Pinkus 171*. The collector reports that the bark of this tree, which is uncommon in collections, is used as a fish poison.

MALPIGHIACEAE

BLEPHARANDRA HYPOLEUCA (Benth.) Griseb. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 28, 211*. This monotypic genus

appears to have been previously known only from the vicinity of Mount Roraima.

VOCHYSIACEAE

Vochysia Pinkusii A. C. Smith, sp. nov. Arbor ad 20 m. alta, trunco ad 30 cm. diametro; ramulis juventute quadrangulatis ferrugineo-subadpresso-hirsutis demum glabrescentibus; foliis oppositis, petiolis 10–15 mm. longis mox glabris, laminis coriaceis siccitate supra olivaceis oblongo-ellipticis, 10–14 cm. longis, 5.5–7.5 cm. latis, basi subacutis vel obtusis et in petiolum decurrentibus, apice cuspidatis vel breviter acuminatis (acumine 4–8 mm. longo obtuso), margine integris et leviter recurvatis, supra glabris, subtus brevissime et densissime ferrugineo-tomentellis demum glabrescentibus, costa ad apicem valida supra conspicue impressa subtus prominente, nervis secundariis utroque 15–20 patentibus curvatis prope (1–2 mm.) marginem conspicue anastomosantibus supra impressis subtus prominentibus, venulis inconspicuis; inflorescentiis terminalibus 1–3 racemiformibus 15–20 cm. longis; rhachide crassa ut ramulis hirsuta, pedunculis brevibus (ad 5 mm. longis) vel nullis, floribus binis vel solitariis; pedicellis gracilibus 8–13 mm. longis paullo infra medium decidue bracteolatis, cum calyce ferrugineo-hirsutis (pilis 0.2–0.3 mm. longis patentibus); calycis laciniis quatuor ovato-deltoideis, 1.7–2.2 mm. longis et latis, intus glabris, apice obtusis, postica curvata plicata oblongo-lanceolata, calcare excepto 18–22 mm. longa, expansa 8–10 mm. lata, calcare gracili subrecto 7–8 mm. longo; petalis jam delapsis non visis; stamine dense ferrugineo-sericeo (pilis ad 0.5 mm. longis), filamento crasso 1–1.5 mm. longo, anthera crassa (circiter 1.5 mm. diametro) 16–18 mm. longa, facie ventrali concava, apice obtuse conica; ovario dense sericeo, stylo crasso 14–17 mm. longo basin versus parce sericeo excepto glabro, stigmate subcapitato.

Type, *Pinkus 167*, collected January 22, 1939, in mixed forest along Maurukow Creek, headwaters of Rio Cotinga near Venezuelan boundary, drainage of Rio Branco, State of Amazonas, Brazil. The new species falls into the Series *Ferrugineae*, in which it seems most closely related to *V. majuscula* Pilger of Amazonian Peru, a species very similar to ours in foliage, but with a curved and conspicuously thicker calyx-spur and a glabrous ovary. Another close relative of the new species is *V. densiflora* Spruce of the Rio Uaupes region, but, in comparison with ours, that species has obovate leaves, secondary nerves which are straighter, more distant, and less spreading, and a much stouter calyx-spur.

EUPHORBIACEAE[1]

Mabea argutissima Croizat, sp. nov. Arbor gracilis ad 4 m. alta, innovationibus pube indutis sub lente crispule lanulosa, tomentum badium haud continuum efformante, serius glabritis, cortice laeviusculo brunneo; folia

[1] By L. Croizat.

exacte elliptica, apice subabrupte caudato-cuspidata, basi subrotundata, 5–9 cm.
longa, 1.5–2.5 cm. lata, firme çhartacea, brunneo-olivacea subconcoloria, pilis
raris ad basin nervii medii exceptis tota glaberrima, margine primo intuito
eroso, oculo armato eximie serrulato, dentibus adpressis ciliato-setaceis ad 7
per centimetrum, nervis circiter 10-jugis, more generis late patentibus laxe
laqueatis, petiolo gracili circiter 3 mm. longo, hispidulo supra in apice obscuris-
sime glanduloso, glandulis lente inquirendis, stipulis petiolaribus subtri-
angularibus setaceis, rectis vel apice incurvatis, margine laevissime glanduloso-
ciliatis, puberulis, ad 9 mm. longis; capsula ellipsoidea trigona, 1.6 cm. longa,
1.4 cm. lata, vix puberula, pericarpio coriaceo griseo laevissimo, in apice basi
columnae stylaris indurata apiculata, calyce sub fructu 3 mm. lato, lobis tri-
angularibus abrupte acuminatis, semine ellipsoideo, 7 mm. longo, 4 mm. lato,
submaturo badio, laevissimo, raphide nigro perspicuo, columella fructu delapso
11 mm. longa.

Type, *Pinkus 275*, collected January 19, 1939, in the vicinity of Ara-
bupu, Mount Roraima District, Venezuela, alt. 4200 ft., and deposited in
the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard.,
etc.). "Slender tree in second growth, 12 ft. high; trunk 5 in. diam.; fruit
green." Although the type locality of *M. biglandulosa* Baill. is also the
vicinity of Mount Roraima, the present species is easily distinguished from
Baillon's. I have not seen an authentic specimen of *M. biglandulosa*, but
Pax and Hoffmann (Pflanzenreich 4(147)[5]: 34. 1912) characterize it as
"Arbor scandens; ramuli . . . glabri; . . . limbus . . . integer," which dif-
ferentiates it from *M. argutissima*. It may be suspected that the new
species belongs in the Section *Umbelluliferae* Pax & Hoffmann, but the
material is too scanty to authorize even provisional statements. The
combination of pubescence with a fine subaristate serration is not common
in *Mabea*, according to the available material and the literature.

CUNURIA SPRUCEANA Baill. British Guiana: Membaru Creek, upper
Mazaruni River, *Pinkus 236*; a tree in mixed forest, 70 ft. high; trunk 16
inches diameter; latex white. To the best of my knowledge the genus has
not previously been reported from British Guiana, the four species thus
far known being from the Rio Negro and Solimoes basins of Brazil. Com-
pared with typical material of *C. Spruceana*, our specimens (in fruit) have
slightly larger leaf-blades, which are truncate or faintly cordate at base,
and larger capsules (to 6 cm. long).

Cunuria Gleasoniana Croizat, sp. nov. Arbor ad 20 m. alta, innovationi-
bus sub lente hic inde pube nigrescente hispidulis, caeterum cortice glabrato
crebre ruguloso sordide brunneo indutis, cicatricibus foliorum delapsorum
5 mm. longis et 3.5 mm. latis notatis; folia obovata vel elliptico-rotundata ad
elliptica, 11–17 cm. longa, 7–8 cm. lata, coriacea, supra brunnea, subtus pube

brevissima arcte adpressa straminea interdum sublucida optime induta, basi subrotundato-cuneata, margine integra revoluta, trabeis conspicuis utrinque reticulatim venosa, venis penninerviis utrinque conspicuis interdum pilis simplicibus nigris tenuissimis, lente acri inquirendis, vestitis, 7–10-jugis, arcuato-adscendentibus, sub marginem ipsum tenuiter anatomosantibus, glandulis supra ad laminae basin 2 more generis late impresso-crateriformibus omnino sessilibus, petiolo valido toto ruguloso 1.5–3 cm. longo; inflorescentia ♂ haud visa sed ut videtur subapicali, forsan subgraciliter, paniculata vel cymulosa; inflorescentia ♀ subterminali (i. e. ex axillis ipsis summis) verosimiliter breviter spicato-cymosa ad 3 cm. longa, parcius adpresso-tomentosa, crassiuscula, ad 2 mm. basi diametiente, floribus 5–6 onusta; capsula submatura soluta tantum visa, epicarpio secedenti carnosula laevi, pube sericea more folii plus minusve induto, coccis solutis duris ad 18 mm. longis, semine immaturo laevissimo subtetragono rotundato ad 8 mm. lato, caruncula cerina magna, foveolis 4 circumambientibus in centro nempe cruciformibus.

Type, *Pinkus 176*, collected February 4, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, British Guiana, alt. 2000 ft., and deposited in the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard., etc.). Another collection is *Pinkus 234*, from Membaru Creek, upper Mazaruni River. The species is named for Dr. H. A. Gleason, in recognition of his important work on the flora of the region.

Although a definite identification of *Cunuria* requires full material, with staminate and pistillate inflorescences, there seems no doubt that this is the genus represented. The details of seed structure and capsule shown by Mueller (Mart. Fl. Bras. 11 (2): *pl. 14, f. 2.* 1874) fully agree with those of our plant. *Glycydendron* has an altogether different fruit. Of the known species of *Cunuria*, none seems to have the peculiar pubescence of *C. Gleasoniana*. The close, silky, pale yellow, and apparently fairly persistent indument of the lower surface of the leaf suggests that of certain Leguminoseae and is very rarely found in Euphorbiaceae. The scattered, very thin, blackish hairs sometimes found cloaking the midrib and the larger veins are also characteristic of the new species.

Croton roraimensis Croizat, sp. nov. Arbor ad 10–13 m. alta, trunco ad 80 cm. diametro, innovationibus pube sordida fasciculata, lepidibus subcrustaceis discoloribus taetris; folia subcoriacea firma brunneo-olivacea ovato-elliptica, 11–20 cm. longa, 4–9 cm. lata, sensim in apicem acuminata, basi subcuneato-rotundata, lepidibus argillaceis sparsis utrinque asperula, ex alabastro vix deprompta indumento cerino-lepidoto tota induta, adulta fere glabra, margine revoluto subsimpliciter crenato-serrato, dentibus subincurvis callosopuberulis ad 2 per centimetrum, nervo medio valido, venis lateralibus irregulariter circiter 7-jugis, modice patentibus, optime anatomosantibus, petiolo

valido 2.5–4.5 cm. longo tomentoso-hispido, subtus in apice glandulis utrinque 1 vel 2 ceraceis breviter stipitatis ornato, stipulis e basi lata setaceis integris rigidiusculis ad 8 mm. longis; cyma ♂ : floribus conferte glomerulatis, pedunculo ad 8 mm. longo, rhachide ad 2 mm. crassa sub lente grosse tomentosa; calyce patente 1 cm. lato tenuissime tomentoso vel subglabro, lobis subovatis ad 4 mm. longis; petalis glabris, calycis lobis subaequilongis, circiter 1 mm. latis, margine laevissime ciliato-lanulosis; staminibus ad 20, basi pilosis, pro more generis minutis, vix 7.5 mm. longis; cyma ♀ : calyce 8 mm. lato profunde partito vix accrescente, basi tomentello, supra glabrescente, stipite crassiusculo 2 mm. longo fulto, lobis late triangularibus ad 2 mm. longis, totidem ad basin latis; capsula pro more generis magna, 2 cm. longa, circiter 1.5 cm. lata, ellipsoidea, laevissime tantum trigona, tota tomento lepidoto subaureo induta, sub lente pilis fasciculatis hic inde hirtula, epicarpio crustaceo subtenui.

Type, *Pinkus 122*, collected January 6, 1939, on southwestern slopes of Mount Roraima, Venezuela, alt. about 7400 ft., and deposited in the herbarium of the Arnold Arboretum (dupl. in Herb. N. Y. Bot. Gard., etc.). Another collection from the same locality is *Pinkus 134*. The type is from a pistillate plant, the other collection from a staminate plant. It is a very distinct species, with affinities in the direction of *C. cuneatus* Kl., *C. surinamensis* Muell. Arg., and *C. matourensis* Aubl., from which it is easily distinguished by the elliptic or elliptic-ovate leaves, mostly rounded at the base, and by the indument. A close relationship is also suggested with the Peruvian *C. Tessmannii* Mansf., which, however, seems to be only remotely related to *C. hemiargyreus* Muell. Arg. as suggested by Mansfeld (Notizbl. Bot. Gart. Berlin 9: 265. 1927).

STERCULIACEAE

STERCULIA GUIANENSIS Sandwith. British Guiana: near Makreba Falls, Kurupung River, upper Mazaruni region, *Pinkus 15*. Excellent flowering specimens from the type locality.

OCHNACEAE[1]

Sauvagesia Imthurniana (Oliver) Dwyer, comb. nov. *Leitgebia Imthurniana* Oliver, Trans. Linn. Soc. II. 2: 271. 1887. *Roraimanthus Imthurnianus* Gleason, Phytologia 1: 39. 1933. Venezuela: Mount Roraima, summit, *Tate 400; Pinkus 116*. Mount Auyan-tepui, summit, *Tate 1130*.

All the characters of this plant indicate its position in the genus *Sauvagesia*, although previous workers have not considered it in relation to this genus. It is well marked specifically by its densely imbricate leaves and its flowers being borne on very short pedicels. The facts that the placentation of the ovary is parietal and that the staminodia of the inner

[1] In part by J. D. Dwyer.

corona are free to the base are verified by a careful examination of new and earlier material; thus the necessity for the genus *Roraimanthus* ceases to exist. Although it bears a superficial resemblance to *Leitgebia guianensis* Eichl. in having the leaves densely imbricate, the present plant differs in having the ovules attached basally and in lacking the outer ring of spatulate staminodia.

S. Imthurniana resembles *S. fruticosa* Mart. & Zucc. in the type of leaf, which is coriaceous and imbricate, with prominent, strongly ascending, striate veins.

Ouratea mazaruniensis A. C. Smith & Dwyer, sp. nov. Frutex vel arbor parva ubique glabra; ramulis teretibus crassis cinereis juventute plus minusve striatis; petiolis rugosis valde incrassatis (2–3 mm. diametro) 1–4 mm. longis; laminis tenuiter coriaceis vel chartaceis siccitate olivaceis vel fuscis, plus minusve concoloribus et supra interdum nitidis, elliptico- vel ovato-oblongis, (5–)7–12.5 cm. longis, 2.5–5 cm. latis, basi plerumque subcordatis interdum rotundatis vel late obtusis, apice rotundatis vel obtusis interdum emarginatis, margine regulariter et inconspicue crenulato-serratis (serrationibus 6–9 per centimetrum obscure calloso-apiculatis), costa supra elevata subtus prominente, nervis secundariis utroque 7–12 arcuatis marginem versus valde adscendentibus subtus prominulis supra subimmersis, venulis supra obscuris subtus paullo prominulis vel planis; paniculis pauciramosis terminalibus vel subterminalibus ad 10 cm. longis (quam foliis apicem ramulorum versus paullo longioribus); bracteis papyraceis oblongis acutis 3–6 mm. longis vel interdum foliaceis; pedicellis gracilibus sub anthesi curvatis 7–10 mm. sub fructu rectis ad 13 mm. longis; sepalis oblongo-ellipticis, 6–7.5 mm. longis, 2.5–3.5 mm. latis, apice obtusis vel minute apiculatis, exterioribus coriaceis interdum anguste scariosomarginatis, interioribus praeter lineam medianam dorsalem coriaceam membranaceis luteis; petalis luteis tenuiter papyraceis vel membranaceis, late obovatis, 6–7.5 mm. longis, 5–7 mm. latis, basi valde contractis, apice rotundatis et interdum leviter emarginatis, conspicue nervatis, venulis flabellatim recurvatis; antheris sessilibus luteis subulatis valde transverse rugosis 5–6 mm. longis; gynophoro cylindrico sub anthesi 1–1.2 mm. longo et 0.7–1 mm. diametro; carpidiis 5 ovoideis 0.5–0.9 mm. longis; stylo gracili 4–5 mm. longo truncato; gynophoro sub fructu obovoideo ad 7 mm. longo et 4 mm. diametro; drupis paucis (saepe solitariis) oblongo-ovoideis ad·8 mm. longis et 6 mm. latis.

Type, *Pinkus 185*, collected February 2, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., British Guiana. Another collection from the same region is *Pinkus 278*. The new species is characterized by its short-petiolate leaves (appearing at first glance subsessile), of which the blades are usually rounded at apex and lightly cordate at base. It appears to be without close relatives, but in foliage may be compared with the Brazilian *O. glaucescens*

(St. Hil.) Engl., a species with a simpler inflorescence, stouter pedicels, slightly larger flowers, and more numerous carpels. On the basis of inflorescence characters the new species is doubtless more closely related to such species as *O. roraimae* Engl. and *O. rigida* Engl., but these are very different in foliage.

CARYOCARACEAE

ANTHODISCUS OBOVATUS Benth. British Guiana: Membaru Creek, upper Mazaruni region, *Pinkus 233;* Arubaru River (Kako tributary), upper Mazaruni drainage, near Mount Haiamatipu, *Pinkus 280.* The species is apparently new to Guiana, having previously been known from the Rio Negro region of Brazil. Our specimens have the leaflets conspicuously emarginate at apex, the flowers large (petals to 9 mm. long; filaments to 7 mm. long), and the immature fruits smooth rather than sulcate. However, they seem to fall into a reasonable concept of the species.

THEACEAE

ARCHYTAEA MULTIFLORA Benth. British Guiana: Arubaru River (Kako tributary), Mazaruni drainage, near Mount Haiamatipu, alt. about 2000 ft., *Pinkus 175.* Hitherto known from Mount Roraima, Mount Duida, and adjacent Brazil.

GUTTIFERAE

CLUSIA MELCHIORI Gleason. Venezuela: Mount Roraima, southwestern slopes, in damp forest, alt. about 7400 ft., *Pinkus 161.* Previously known from Mount Duida; like the type, our specimen bears young fruits.

Tovomita albiflora A. C. Smith, sp. nov. Arbor glabra ad 8 mm. alta, ramulis conspicue rugosis subteretibus vel apicem versus compressis; petiolis crassis 1.5–3 cm. longis basi incrassatis ut ramulis rugosis et mox saepe purpurascentibus; foliorum laminis chartaceis ellipticis, (9–)12–20 cm. longis, (3–)4–6.5 cm. latis, basi acutis vel subattenuatis, apice acutis vel obtuse et breviter cuspidatis, margine cartilagineis integris, supra viridibus, subtus saepe paullo pallidioribus, costa valida utrinque prominente et striata, nervis lateralibus primariis utroque 9–13 arcuatis marginem versus (2–3 mm.) abrupte curvatis et inconspicue anastomosantibus, nervis secundariis lateralibus paucis inconspicuis, venulis copiose reticulatis utrinque prominulis; inflorescentiis masculis terminalibus sessilibus multifloris ad 3 cm. longis et 5 cm. latis, e basi 4- vel 5-ramosis, ramulis primariis 9–13 mm. longis valde compressis 2–4 mm. crassis rugosis conspicue lenticellatis, in cymas 3-floras desinentibus; bracteis tenuiter coriaceis oblongis acutis 5–7 mm. longis; pedicellis crassis (circiter 2 mm. diametro) rugosis 3–6 mm. longis, 2 lateralibus basin versus articulatis et bibracteolatis (bracteolis papyraceis oblongo-ovatis carinatis, circiter 4 mm. longis, apice subacutis, basi alte connatis); sepalis 4 chartaceis, 2 exterioribus semiorbiculari-ovatis, 4–5 mm. longis et latis, apice rotundatis,

florem involventibus, 2 interioribus oblongis, 2–3 mm. latis; petalis 4 tenuiter carnosis oblongis, 4–5 mm. longis, 2–3 mm. latis, apice rotundatis; staminibus 40–45, 3–4.5 mm. longis, filamentis crassis (0.5–0.6 mm. diametro), antheris 0.5–0.6 mm. longis, quam filamentis haud latioribus; inflorescentiis femineis 3–6 cm. longis et latis, 9–15-floris, pedunculatis (pedunculo 8–15 mm. longo), ramulis primariis 3 et pedunculo inflorescentiarum mascularum ramulis similibus; bracteis bracteolis et perianthio eis florum masculorum similibus sed paullo majoribus (pedicellis ad 8 mm. longis, petalis ad 7 mm. longis et 4 mm. latis); staminodiis staminibus similibus; ovario cylindrico conspicue striato, stigmatibus 4 conspicuis subsessilibus subpeltatis; fructibus subpyriformibus coriaceis rugosis conspicue lenticellatis, maturitate 3–3.5 cm. longis et 1–1.5 cm. diametro, basin versus contractis, apice attenuatis, stylis 4 crassis brevibus connatis sub stigmatibus articulatis; reliquis floris sub fructu saepe persistentibus.

Type, *Pinkus 269*, collected January 19, 1939, in the vicinity of Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft. The collector reports that the Arekuna name is "wakome," and that the flowers are fragrant, with white petals and stamens. *T. albiflora* closely resembles *T. rubella* Spruce, from the Rio Negro of Brazil, in its leaf-texture and venation, but has the leaf-blades more distinctly elliptic and less gradually tapering at base. The most distinguishing characters of the new species are found in the stout rugose lenticellate inflorescence-branches and the short stout pedicels; these features contrast with the smooth and slender corresponding parts of *T. rubella*, which also has. fewer stamens than the new species. Another species of this relationship is *T. calodictyos* Sandwith, of British Guiana, which has the leaves essentially similar but with 16–22 primary lateral nerves, smooth inflorescence branches, and fewer stamens.

PASSIFLORACEAE[1]

PASSIFLORA CARDONAE Killip. British Guiana: Membaru Creek, upper Mazaruni River, *Pinkus 38*. Previously known only from the type collection from Mount Auyan-tepui, Venezuela.

MELASTOMATACEAE[2]

MICONIA MEGAPHYLLA Gleason. British Guiana: Adaro River (Kukui tributary), upper Mazaruni drainage, near Mount Wupaima, *Pinkus 164*. New to British Guiana; previously known only from subandean Bolivia.

MYRSINACEAE

Conomorpha sessilis A. C. Smith, sp. nov. Arbor ad 5 m. alta, trunco ad 15 cm. diametro; ramulis subteretibus cinereis juventute densissime et arctissime ferrugineo-tomentellis mox glabris; petiolis 12–18 mm. longis supra

[1] By E. P. Killip.
[2] By H. A. Gleason.

leviter canaliculatis juventute ut ramulis tomentellis; laminis chartaceis vel
tenuiter coriaceis siccitate subglaucis vel fuscis oblongo- vel leviter obovato-
oblongis, 8–10.5 cm. longis, 3–4.5 cm. latis, basi acutis et in petiolum decur-
rentibus, apice cuspidatis vel breviter acuminatis (acumine 5–10 mm. longis
obtusis), margine integris et anguste sed conspicue revolutis, supra punctulis
innumeris nigris obscure obtectis, subtus dense ferrugineo-lepidotis, costa supra
leviter insculpta subtus prominente, nervis secundariis numerosis (utroque 15–
20) leviter arcuatis et marginem versus anastomosantibus utrinque haud
prominulis; inflorescentiis subpyramidatim paniculatis 3–4 cm. longis ubique
praeter corollam densissime ferrugineo-lepidotis; pedicellis 0.8–1.2 mm. longis;
calycis lobis fere ad basin liberis 4 vel 5 oblongo-deltoideis, 0.7–0.9 mm. longis,
subacutis, parcissime punctatis, intus glabris; corolla lutea glabra 2–2.2 mm.
longa, lobis 4 (raro 5) ovatis, circiter 1.3 mm. longis et latis, apice obtusis,
basi leviter contractis, parcissime nigro-punctatis; staminibus basi corollae
loborum insertis, filamentis subnullis, antheris luteis oblongo-deltoideis 0.8–
0.9 mm. longis dorso parcissime glandulosis; ovario sub anthesi circiter 0.5 mm.
diametro pallide lepidoto, stylo crasso circiter 1 mm. longo truncato.

Type, *Pinkus 55*, collected December 12, 1938, along Arabupu River
near Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft. *C. ses-
silis* appears to be most closely related to *C. punctata* Mez, also of the
Mount Roraima region, from which it differs in its narrower and thicker
leaves, shorter pedicels, smaller and usually 4(rather than 5- or 6)-merous
flowers, and its even less conspicuous filaments. The specific name refers
to the essentially sessile anthers.

Conomorpha gracilis A. C. Smith, sp. nov. Arbor ad 7 m. alta, trunco
ad 15 cm. diametro; ramulis crassis cinereis subteretibus juventute arctissime
cano-pulverulentibus mox glabris; petiolis subteretibus gracilibus 12–20 mm.
longis mox glabris; laminis tenuiter coriaceis siccitate utrinque viridibus vel
olivaceis ellipticis vel obovato-ellipticis, (4–)6–9 cm. longis, (2–)3–5 cm.
latis, basi acutis vel attenuatis et in petiolum decurrentibus, apice obtusis vel
rotundatis et saepe minute emarginatis, margine integris et leviter recurvatis,
utrinque glabris, supra punctulis paucis nigris obscure obtectis, subtus dissite
et immerse punctulatis, costa valida supra elevata subtus prominente, nervis
secundariis utroque 12–18 patulis prope marginem anastomosantibus cum rete
venularum utrinque valde prominulis; inflorescentiis racemosis 4–10.5 cm.
longis 20–35-floris breviter stipitatis, cum foliis apices ramulorum versus con-
gestis, ubique praeter corollam parce ferrugineo-puberulis; bracteis lineari-
oblongis 1.3–1.8 mm. longis; pedicellis 1–2 mm. longis; calyce cupuliformi
circiter 1.3 mm. longo, lobis 4 deltoideo-ovatis, circiter 0.9 mm. longis et 1.1 mm.
latis, apice obtusis, margine integris et minute ciliolatis, intus glabris, obscure
punctulis nigris paucis (2 vel 3 per lobum) pictis; corolla lutea 3.5–4.5 mm.
longa basin versus glabra, lobis 4 oblongis, 1.8–2.6 mm. longis, 1.4–2.2 mm.

latis, apice obtusis, intus dense papilloso-puberulis, extus glabris vel parcissime puberulis; staminibus basi corollae loborum insertis, filamentis complanatis circiter 0.5 mm. longis, antheris oblongo-deltoideis, 1.1–1.3 mm. longis, saepe recurvatis, basi cordatis, apice obtusis; ovario dense pallide lepidoto conico sub anthesi 0.5–0.7 mm. diametro, stylo gracili 1–1.5 mm. longo apice leviter incrassato.

Type, *Pinkus 181*, collected February 2, 1939, along Arubaru River (Kako tributary), upper Mazaruni drainage, British Guiana, alt. about 2000 ft. In the essential characters of the long racemose inflorescences, large 4-merous flowers, obvious filaments, lepidote ovary, and slender tapering style, *C. gracilis* resembles *C. grandiflora* Mez, of the Rio Negro region of Brazil, doubtless its closest ally. The new species differs from *C. grandiflora*, however, in its proportionately broader leaves, which are concolorous rather than reddish beneath and which have a more conspicuous venation. The calyx-lobes of *C. grandiflora* are proportionately longer than those of *C. gracilis* and more obviously punctate. The specific name of the new species refers to the long slender inflorescence.

Rapanea roraimensis A. C. Smith, sp. nov. Arbor glabra ad 10 m. alta, trunco ad 20 cm. diametro; ramulis subteretibus cinereis striatis; petiolis rugosis 7–10 mm. longis supra leviter canaliculatis superne anguste alatis; laminis chartaceis siccitate olivaceis concoloribus anguste ellipticis, 11–16 cm. longis, 3–5 cm. latis, basi attenuatis, apice acutis (apice ipso saepe obtuso et mucronulato), margine integris et leviter recurvatis, utrinque inconspicue et dispersissime punctatis, costa supra elevata et leviter canaliculata subtus prominente et striata, nervis secundariis utroque 12–20 subpatulis cum rete venularum conspicuo irregulariter anastomosantibus et utrinque prominulis; inflorescentiis fasciculatis vel e ramulis verruciformibus (pedunculo crasso ad 4 mm. longo) 5–10-floris formatis; bracteis deltoideis 1–1.3 mm. longis subacutis minute ciliolatis; florum femineorum pedicellis rugosis crassis 1.3–2.6 mm. longis; calyce erecto-patente, lobis 5 fere ad basin liberis deltoideo-ovatis, 0.7–0.9 mm. longis et latis, apice obtusis vel rotundatis, margine minute ciliolatis, parce nigro-punctatis et interdum lineolatis; corolla subrotata sub anthesi 3.5–4.5 mm. diametro, lobis 5 elongato-deltoideo-oblongis, 1.5–1.8 mm. longis, 0.8–1.1 mm. latis, apice obtusis, margine minute puberulo-ciliolatis, dense fusco-glanduloso-lineolatis; staminibus quam corollae lobis paullo brevioribus, antheris sessilibus oblongis 1–1.2 mm. longis, basi sagittatis, apice subacutis; ovario laevi glabro cylindrico, circiter 1.3 mm. longo et 0.9 mm. diametro; stigmate cylindrico circiter 1.5 mm. longo, apice irregulariter lobato-crenato.

Type, *Pinkus 132*, collected January 11, 1939, in damp forest on southwestern slopes of Mount Roraima, Venezuela, alt. about 7800 ft. The new species is characterized by its glabrous habit, chartaceous nar-

rowly elliptic leaf-blades with prominulous venation, and comparatively long pedicels. Among the species known to me from herbaria, descriptions, and Mez's treatment in the Pflanzenreich, it seems most closely related to *R. lancifolia* (Mart.) Mez and *R. umbellata* (Mart.) Mez, both of southern Brazil. From the former it differs by its larger leaves and flowers and narrower corolla lobes, from the latter by its thinner, duller, and somewhat more pointed leaf-blades, and its shorter pedicels. Although *R. roraimensis* bears a slight resemblance to some of the specimens placed with *R. guyanensis* Aubl. in herbaria, it obviously differs in many respects from the typical form of that species, which has thick obovate-elliptic leaf-blades with immersed venation and rounded or obtuse apices, and very short pedicels.

Rapanea resinosa A. C. Smith, sp. nov. Frutex glaber ad 1 m. altus; ramulis subteretibus striatis juventute castaneis demum cinereis; petiolis rugosis 5–10 mm. longis superne anguste alatis; laminis chartaceis siccitate fusco-olivaceis concoloribus lineari-ellipticis, 5–11 cm. longis, 1.3–3 cm. latis, basi attenuatis, apice gradatim acutis (apice ipso saepe obtuso et calloso), margine leviter recurvatis et integris vel apicem versus leviter crenulatis, utrinque plerumque lineis resiniferis perlongis (saepe obscure) auctis et disperse (supra impresso-) punctatis, costa supra elevata subtus prominente, nervis secundariis utroque 8–12 subrectis adscendentibus utrinque prominulis, rete venularum plerumque inconspicue prominulo; inflorescentiis fasciculatis vel e ramulis verruciformibus (pedunculo ad 2 mm. longo) 7–15 floris formatis; bracteis deltoideis circiter 1 mm. longis subacutis ciliolatis; pedicellis crassis 2–3 mm. longis; floribus masculis: calyce patente, lobis 5 fere ad basin liberis ovato-deltoideis, 0.9–1.1 mm. longis et latis, apice subacutis vel obtusis, margine minute et regulariter glanduloso-ciliolatis, parce nigro-punctatis (punctulis 2–6 per lobum); corolla rotata sub anthesi 6–7 mm. diametro, lobis 5 (raro 6) oblongis, 2.2–3 mm. longis, 1.3–1.5 mm. latis, apice obtusis vel rotundatis, margine minute puberulo-ciliolatis, parce nigro-punctatis (punctulis saepe paullo elongatis sed haud lineolatis); staminibus quam corollae lobis brevioribus, antheris sessilibus oblongo-ovoideis, 1.7–2 mm. longis, obtusis, crassis; ovario laevi conico, stigmate sessili punctiformi; floribus femineis: corolla quam mascula paullo minore, lobis 1.7–2 mm. longis, haud punctulatis; antheris elongato-deltoideis circiter 1 mm. longis, basi sagittatis, apice subacutis; ovario subgloboso sub anthesi 1–1.5 mm. diametro, minutissime aureoglanduloso; stigmate sessile morchelliformi ovarium subaequante; fructibus subglobosis atris 3–4 mm. diametro, stigmate persistente coronatis.

Type, *Pinkus 84*, collected January 17, 1939, along Arabupu River, near Arabupu, Mount Roraima District, Venezuela, alt. 4200 ft.; flower buds greenish, streaked with red. *R. resinosa* is characterized by its glabrous habit and its leaf-blades with resinous lines. Its relationship is with

the Brazilian *R. umbrosa* (Mart.) Mez, from which it differs only in minor details, such as slightly narrower leaf-blades, longer pedicels, and calyx- and corolla-lobes which are not glandular-lineolate. The new species bears a superficial resemblance to the widespread and variable *R. ferruginea* (R. & P.) Mez, but that species has tomentellous young branchlets and a glandular-lineolate perianth, and lacks the resinous lines in the leaf-blades.

<div align="center">APOCYNACEAE[1]</div>

HIMATANTHUS PHAGEDAENICA (Mart.) Woodson. Venezuela: Mount Roraima District, vicinity of Arabupu, alt. 4200 ft., *Pinkus 168*. New to Venezuela; otherwise known from Brazil, from the Rio Negro basin southward to Rio de Janeiro.

<div align="center">RUBIACEAE[2]</div>

CEPHAELIS TATEI Standley. British Guiana: Membaru Creek, upper Mazaruni River, *Pinkus 228*. Previously known from Arabupu, Mount Roraima District, Venezuela.

LADENBERGIA PITTIERI Standley. British Guiana: Adaro River (Kukui tributary), upper Mazaruni drainage, near Mount Wupaima, alt. about 3000 ft., *Pinkus 170*. Previously reported from Andean Venezuela and eastern Colombia.

Psychotria mazaruniensis Standley, sp. nov. Arbor 6-metralis, trunco 7.5 cm. diam., omnino glabra, ramulis gracilibus teretibus in sicco fere nigris atque infra nodos valde constrictis; stipulae persistentes erectae 7–9 mm. longae inferne in vaginam connatae, parte libera utroque latere biloba, lobis vagina brevioribus obtusis vel subrotundatis atque setoso-mucronatis; folia magna petiolata firme membranacea, petiolo gracili 2–2.5 cm. longo; lamina oblongo-ovalis 15–20 cm. longa 6.5–9 cm. lata apice rotundata atque subito cuspidata, acumine anguste attenuato acuto 1–1.5 cm. longo, basi acuta atque interdum subito contracta, supra in sicco intense olivacea lucida, costa prominula, nervis venisque quoque prominulis vel prominentibus, subtus vix pallidior, sublucida, costa gracili elevata, nervis lateralibus utroque latere ca. 16 prominulis angulo fere recto abeuntibus arcuatis, nervis aliis fere aequaliter prominentibus inter pares adjectis, venulis prominulis laxe reticulatis; inflorescentia terminalis erecta 6 cm. longe pedunculata ca. 4 cm. longa, floribus capitatis, capitulis 5 racemosis dense multifloris breviter pedunculatis ca. 1 cm. diam., bracteis extimis ovato-rotundatis apice late obtusis vel rotundatis ad-pressis glabris; calyx brevis, margine angulato vel brevissime remote denti-culato; corolla alba extus glabra, tubo 8–10 mm. longo crassiusculo infra orem subconstricto, lobis brevibus oblongis obtusis recurvis, extus apice appen-dice albo papilloso auctis.

[1] By R. E. Woodson.
[2] By P. C. Standley.

Type, *Pinkus 14*, collected September 13, 1938, on rocky soil on hillside, Kurupung Mountain, near Makreba Falls, upper Mazaruni region, British Guiana, and deposited in the herbarium of the Field Museum (dupl. in Herb. N. Y. Bot. Gard., etc.). The corollas in bud are exserted far beyond the bracts. They bear at the apex small, rounded, whitish appendages that afford a striking character for recognition of the species. The plant might be referred equally well, perhaps, to the genus *Cephaelis*.

COMPOSITAE[1]

QUELCHIA CONFERTA N. E. Brown. Venezuela: Mount Roraima, summit, alt. 8700 ft., *Pinkus 112*; shrub 3 ft. high; pappus white. Apparently only the second known collection of this endemic monotype. The only corollas on the type material were in bud, and Brown's description does not apply to the mature ones. In these the proper tube is slenderly obconic, rather sparsely pilosulous outside with loose several-celled hairs, and 4 mm. long; the throat is practically lacking, the filaments being inserted only about 0.3 mm. below the apex of the tubular part of the corolla; the 5 equal lobes of the limb are recurved-spreading, linear, obtusish, 5 mm. long. The tails of adjacent anthers are connate for about half their length and are sparsely hispidulous-barbate. The copious whitish-straw-colored pappus bristles are somewhat flexuous, about 3-seriate, hispidulous especially toward base, and somewhat stramineous toward base; they are subequal, with the exception of a very few short outermost ones about 2 mm. long. The style branches are about 1 mm. long, glabrous, oblong, somewhat widened toward the truncate bluntly 2–3-toothed apex, with recurved-spreading tips.

Stenopadus condensatus (Baker) Blake, comb. nov. *Stifftia condensata* Baker in Mart. Fl. Bras. 6 (3): 351. 1884. Venezuela: Mount Roraima, southwestern slopes, alt. about 7200 ft., *Pinkus 157*; shrub 1 ft. high, growing among rocks in open places; bracts and anthers yellowish. The specimens agree well with Baker's description and with a scrap in the U. S. National Herbarium collected by Jenman (no. *10*) in "high stony ground, near Waetipoo M., Cotinga R.," on the Mt. Roraima expedition of 1884–85. The Jenman specimen has broader, obovate leaves, up to 23 × 13 mm., but the differences observed are within the ordinary range of variation of species in this group. A single receptacular pale was found in one of the two heads of the sheet of Pinkus' plant examined, confirming the reference of the species to the genus *Stenopadus*. It is very narrowly linear, 22 mm. long and barely 0.5 mm. wide, somewhat conduplicate, acute, minutely hispidulous-ciliolate toward the tip.

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[1] By S. F. Blake.

Straussia sessilis, a New Species from Hawaii

Otto Degener and E. Y. Hosaka

Rubiaceae are well represented in the Hawaiian Islands. The following species is here described as new:

Straussia sessilis Degener & Hosaka, sp. nov. Paniculis 5–10 mm. longis, corollis glabris et calicibus puberulis.

A small tree 3–7 meters high with leaves clustered at the ends of reddish-brown branches. Leaves glossy, 7–12 cm. long and 3.5–7 cm. wide, on petioles 5–10 mm. long, obovate, entire, glabrous above, sparsely puberulent chiefly between the veinlets below, somewhat obtuse at apex, somewhat acute at base; stipules 4–5.5 mm. long, broadly ovate, obtuse at apex, coriaceous, entire, glabrous on outer surface, densely pilose on inner surface below the middle, caducous. Flowers sessile, usually 10–20 crowded together into a branched cluster about 1.5 cm. high and 2–3 cm. wide having axis 5–10 mm. long, hidden by persistent fleshy stipules. Calyx green, puberulent, 3 mm. wide, 3–5 mm. long with the free 2 mm. limb unevenly and obscurely 5- to rarely 6-toothed, thick. Corolla white, thick, glabrous throughout, about 15 mm. wide, its tube 2–3 mm. long and its acute lobes about 4 mm. long, with throat naked. Free part of filament 1.5 mm. long, glabrous, white; anthers yellow, 1 mm. long; pollen yellow. Ovary 1.5 mm. long, 2 mm. wide, glabrate, whitish; style 2-branched, pubescent, green. Fruit orange, with prominent longitudinal ridges when dried, 10–15 mm. long, 8–10 mm. wide, with exposed obtuse disk about 2 mm. long and 5 mm. wide.

Type locality: North of head of Makua Valley, Oahu. This forest tree, called *kopiko* by the natives, is known only from the Waianae Range of the Island of Oahu, growing here and there north of Mt. Kaala. It is closely related to *S. oncocarpa* Hilleb. *S. sessilis* has a glabrous panicle 5–10 mm. long, a sparsely puberulent calyx and a glabrous corolla; *S. oncocarpa*, on the other hand, has a rusty-pubescent panicle 2.5–5 cm. long and rusty-pubescent calyx and corolla. This new *kopiko* was collected by Forbes (*No. 1808*) on the "slope of Kaala, Mokuleia," April–May, 1912; by Hosaka (*No. 1129 A*) "in semi-moist forest, el. 1700 ft., Mokuleia, Waialua," August, 1933; and by Degener & Salucop (*No. 11,525*) "north of head of Makua Valley, in rain-forest," October 24, 1937. This specimen and thousands of others upon which descriptions for the *Flora Hawaiiensis* or "New Illustrated Flora of the Hawaiian Islands" are based comprise the Degener Herbarium, now deposited on loan at the B. P. Bishop Museum, under the directorship of Dr. Peter Buck. The most complete duplicate set belongs to the New York Botanical Garden.

Waialua, Oahu.

Origin and Development of the Uniseriate Ray in the Coniferae

Elso S. Barghoorn, Jr.

(with 24 figures)

The extensive literature of the anatomy and morphology of the Coniferae[1] contains no complete data on the origin and ontogeny of their ray tissue. It is my intention to review briefly the previous work and to endeavor to clarify certain incompletely investigated points.

1. *Origin of Ray Initials.* The first writers on the details of the origin of cambial ray initials allude to the obscurity of the process (Müller, 1875; Velten, 1875; De Bary, 1884). Müller and Velten made the first efforts to explain the spatial relationships between newly-formed ray initials and the fusiform initials from which they originate. Schmidt (1889) concluded that wood rays of the conifers arise in the cambium by division of fusiform initials. His work, like Müller's and Velten's, was not essentially critical and was not concerned with the cytological mechanism involved. Later, Klinken (1914) in a study of cambial activity in *Taxus baccata* L. affirmed Schmidt's results, but without cytological data. His evidence from serial tangential sections of coniferous phloem was in accord with that which Schmidt obtained from radial sections of the xylem. Thompson's work (1910) was not concerned with the origin and ontogeny of ray tissue in general. This is true also of Chrysler's researches (1913) on the phloem of Pinaceae. Both investigated mature structures and did not deal with phenomena in the cambium.

2. *Ontogeny of Ray Tissue.* Several critical studies have been made of the ontogeny of coniferous rays. That of Jost (1901) is among the earliest, though previously Kny (1884) had noted the marked difference in height of rays between the first annual ring and the older wood of *Pinus sylvestris*. Jost was concerned chiefly with the adjustments of the cambium in the crotch regions of coniferous and dicotyledonous trees. He found that in these regions of pressure and tension the cambium decreased in area, but that individual rays continued to undergo a normal ontogeny as further increments were added.

Klinken, on the other hand, found that by loss of ray initials in the cambium a decrease in height of the rays of *Taxus baccata* might occur. Klinken also confirmed the observations of Zijlstra (1908) and Jost on the splitting of rays by elongating fusiform initials in the cambium.

[1] Nomenclature of Pilger (1926).

Thompson and Holden (1913) and Chrysler (1913, 1915) concerned themselves chiefly with the study of mature xylem and phloem and offered no interpretation of ray ontogeny in terms of cambial activity.

More recently Bannan (1934) made an extensive survey of the different cell types associated with ray origins in representative species of Coniferae and other gymnosperms. He concluded that ray initials "evidently are formed by segmentation of fusiform initials." He did not, however, elaborate upon the details of the process or the cambial changes involved.

In general it may be said that previous researches have dealt with special aspects of these problems and no organized synthesis has yet been made. Much of the work was hampered by preconceived conclusions about the phylogeny of the conifers. Because of this phylogenetic bias, ontogenetic studies were neglected and interpretation was based largely upon a study of mature structures. It should be emphasized that in comparative anatomical work valid phylogenetic conclusions cannot be drawn until ontogenetic processes are reasonably well understood. The following study is primarily concerned with the origin and ontogeny of ray tissue.[1]

MATERIALS AND METHODS

For the most part the technique was that usual in anatomical research. In addition a method was devised whereby large quantities of material might be rapidly and effectively studied. In dealing with fresh, living material fixation and dehydration consume much time and often destroy or obscure detail present in the untreated tissues. A method that employs only aqueous media is therefore preferable. Water-soluble aniline blue as recommended by Crafts (1931) is one of the most satisfactory of these. Instead of glycerin or glycerin jelly commercial corn syrup (Karo) was used for permanent mounts (Monk, 1938). In this way serial tangential sections of xylem or phloem were prepared in a fraction of the time required for dehydration. If the tissues must be stained to render cellular details more plainly visible, safranin added to the water or alcohol used in sectioning is satisfactory. Sections thus prepared are stained on the knife or on the slide just preparatory to mounting. Water-soluble nigrosin is an alternative stain particularly satisfactory for sections of celloidin-embedded woody tissue mounted in corn syrup. Difficulties that arise from a tendency of the stain to clot on the sections after the addition of corn syrup may be overcome by placing the slides over night or for several days in an incubator at 55–60° C. This promotes a more rapid diffusion of the stain and hastens the drying of the slides.

[1] Canal-bearing rays of both conifers and dicotyledons will be treated separately in a later study.

As previously mentioned, it is not possible by a study of the xylem alone to reconstruct accurately the cytological changes involved in the formation of new ray initials. The more or less extensive apical growth of differentiating tracheids markedly alters the cellular relations which existed in the cambium. Also the xylem-forming divisions of newly formed ray initials and of marginal ray initials are frequently sporadic. The xylem derivatives of such initials are therefore spaced at varying distances and do not form radially contiguous series of cells which can be traced in serial tangential sections. In the phloem, on the other hand, there is very little extra-cambial elongation of daughter cells, except for certain fibers, and the phloem derivatives of ray initials are always in series of contiguous cells. In serial tangential sections it is therefore possible to reconstruct the changes which resulted from successive divisions in the cambium.

After a careful study of serial tangential sections the interpretation of radial sections of both xylem and phloem is far more accurate.

ONTOGENETIC STAGES

Ray Origins in the Primary Body

In the primary body of the conifers a definite relation exists between the number of rays that originate in the fascicular and in the interfascicular regions of the stele.[1] As is shown in figure 1, a higher proportion of rays originates in the latter. The anatomical-physiological significance of this relation is not clear, since there are no "foliar rays" or structures in any way related to them in living conifers. However, the existence of such a relation bears directly on the problem of ray ontogeny, since there are distinct differences in size and shape between ray cells that originate in the two different regions. In the interfascicular segments, between the discontinuous protoxylem points of the stem, certain vertically elongated parenchymatous cells are rapidly continuous with the parenchymatous (or tracheary) cells of the wood ray. It would seem, therefore, that certain cells of this so-called medullary crown region give rise to the cambial ray initials, which in turn give rise to the ray tissue of the secondary body. Such "primary ray cells"[2] are vertically elongated and more or less regularly rectangular. This is generally true also of the "primary ray cells" that originate in the fascicular segments of the primary xylem. However, in these segments the parenchymatous cells which give rise to ray initials are much more elongated vertically and are

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[1] In dealing with the primary body the terms fascicular and interfascicular are here used respectively for the primary xylem strands and the intervening parenchymatous tissue.

[2] The term "primary ray cell" refers to those cells of the primary body which, by periclinal division, give rise to ray initials.

arranged in extensive vertical strands closely appressed between the protoxylem tracheids of the primary wood. This position, and the occurrence of the component cells in vertically contiguous series, support the view that the "primary ray cells" of the fascicular segments are derived from the elongated cells of the procambial strands by a series of anticlinal divisions.

There is, therefore, a definite ontogenetic factor in the two types of primary ray origins. "Primary ray cells" that arise in the interfascicular gaps are derived from certain primordial cells of the growing point which did not undergo extensive vertical elongation. In the other type, the "primary ray cells" in the fascicular segments are apparently derived from vertically elongated procambial cells by a series of anticlinal divisions.

The distinction between these two types of primary ray origins is of great importance in the transition from primary to secondary tissue. This is particularly true of the dicotyledons, in many of which the broad multiseriate rays of the secondary body are definitely related to the interfascicular gaps of the primary body. In the conifers, however, the transition to secondary tissue is similar in both the fascicular and interfascicular regions. All the first-formed ray cells of the secondary wood betray a rapid and extensive change in cell size and shape during differentiation. The degree of this change varies greatly in different species, but the qualitative nature of the change is the same in all the Coniferae. The first ray cells that are unquestionably of secondary origin are frequently highly irregular in outline and more or less radially elongated. Elongation occurs independently of the surrounding tissue and tends to separate each cell of a ray from the neighboring component above or below. Thus a series of rays, one, two, or three cells in height, originates from the strand of vertically contiguous members of the primary ray tissue. Also, certain "primary ray cells" fail to divide periclinally and thereby further disrupt the potential vertical extent of the newly-formed rays of the secondary xylem. Two factors are thus involved in the formation of the very low uniseriate rays of the young stem wood of conifers:

(1) the independent development of individual ray initials in the originally vertically contiguous series and

(2) the failure of certain "primary ray cells" in the vertical series to give rise to secondary ray initials.

In the roots the wood rays of corresponding young regions of the secondary axis tend to be considerably higher and frequently more abundant. The increased height is due to a modification of the above two factors. The transition from vertically elongated "primary ray cells" to radially elongated secondary ray cells takes place more slowly. This allows time

for the occurrence in the ray initials of transverse anticlinal divisions which tend to retain the vertical continuity between the individual cells of the ray. Of secondary importance is the greater prevalence of periclinal divisions in the "primary ray cells" of the root than in those of the stem. The quantitative importance of these two factors, which bring about the difference in ray structure of root and stem, varies in different conifers.

The very irregular shape of certain coniferous rays cells has been frequently noted. In general this plasticity of cell form is greatest in the first few annual rings of roots (Figs. 4 and 12) where it may well be considered a concomitant of the peculiar transition from primary to secondary ray tissue. In the change from the "primary ray cells" of the root, derived by septation of vertically elongated procambial cells (Fig. 4), to the normal, radially elongated cells of the secondary body, the individual ray initials undergo extensive changes in cell shape. This often leads to the formation of long projections extended in radial or vertical planes. These irregular cells are most abundantly developed in the roots of the Pinaceae, and are most frequent in *Cedrus*. Figure 4 shows a radial longitudinal section of the root of *Cedrus libanitica* Trew. The completely independent, almost amoeboid development of the newly formed ray cells is readily apparent. Transition to the radially elongated shape is delayed, so that long vertical prolongations of the cells are retained. In figures 3 and 6 these are most frequent between the corners of neighboring tracheids. This relation to the tracheids, seen in transverse sections, suggests a discontinuous system of intertracheary wood parenchyma. The transition to more normal ray structure is illustrated in figure 12.

In connection with ray ontogeny in coniferous roots, it is interesting to note the ray structure of the Carboniferous genus *Sphenophyllum*. Scott (1920) considered the secondary xylem of certain species of *Sphenophyllum* to have a unique system of intertracheary wood parenchyma. In transverse sections of favorably preserved specimens parenchymatous elements are interspersed between the rounded corners of adjacent tracheids in an apparently discontinuous manner (Fig. 2). However, in radial longitudinal sections, these parenchymatous cells possess radially oriented projections which connect the individual cells in the semblance of wood rays. If we compare with *Cedrus* roots, it seems clear that this anomalous parenchyma is the result of a delayed transition from primary to secondary ray tissue. Owing to the modified ray ontogeny in the secondary body of *Sphenophyllum*, the appearance of an intertracheary system of wood parenchyma is more pronounced than in coniferous roots, but the difference is purely quantitative. I have seen similar structure in the roots of *Medullosa* and of *Cordaites*.

Ray Origins in the Secondary Body

The cambium of the conifers or of the dicotyledons is composed of two distinct types of cells, the large, vertically elongated or fusiform initial, and the much smaller, nearly isodiametric ray initial. The fusiform initials of the conifers give rise to the tracheids and wood parenchyma of the xylem, and to the sieve tubes, parenchyma and fibers of the phloem. The ray initials form the ray tissue of both xylem and phloem. With the rapid increase in girth that results from secondary growth, the vascular rays that originated in the primary body become more and more widely separated. New rays of secondary origin are formed by the lateral meristem as the primary rays diverge. These originate in the cambium by cellular changes in the fusiform initials. The nature of these changes is quite complex, and difficult to ascertain. It seems clear that there are four quite distinct types of ray origins in the secondary body, which, taken collectively, account for all the varied ray structures found in the Coniferae. These are as follows:

(1) a single ray initial formed at the end of a fusiform initial;
(2) a single ray initial formed at the side of a fusiform initial;
(3) a vertical series of individual ray initials derived by segmentation of a fusiform initial;
(4) one or more vertically adjacent single-celled rays formed by xylem divisions of those initials which on the phloem side give rise to the so-called radial plates.

From this it follows that most ray origins in the secondary body are single cells. Indeed, it is quite rare in the older (i.e., later-formed) wood of conifers to find ray origins of more than one initial. On the other hand,

Explanation of Figures 1–6

Fig. 1. *Keteleeria Davidiana* (Bertr.) Beissn. Transverse section of stem showing relation of primary ray origins to the fascicular and interfascicular segments of the primary body. ×50.

Fig. 2. *Sphenophyllum plurifoliatum* Will. and Scott. Transverse section. Cellulose nitrate peel, Iowa coal ball. Note the apparent discontinuity of rays similar to that illustrated in figure 6. ×13.

Fig. 3. *Cedrus libanitica* Trew. Transverse section of a root showing apparent discontinuity of rays in early formed secondary xylem. A transverse view of the structure shown in figure 4. ×100.

Fig. 4. *Cedrus libanitica.* Radial longitudinal section of root showing ray origin from "primary ray cells" of the root. Note the extremely irregular shape of ray cells, with their radial and vertical prolongations. ×100.

Fig. 5. *Cupressus macrocarpa* Gordon. Radial longitudinal section of root showing the origin of two new rays and the increase in height of the rays by transverse anticlinal divisions. ×100.

Fig. 6. *Cedrus libanitica.* Transverse section of a root showing apparent discontinuity of rays in early formed secondary xylem. ×35.
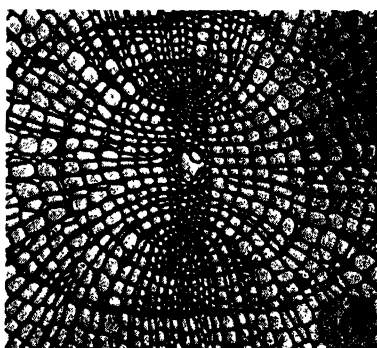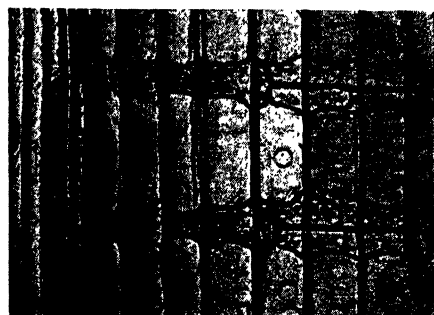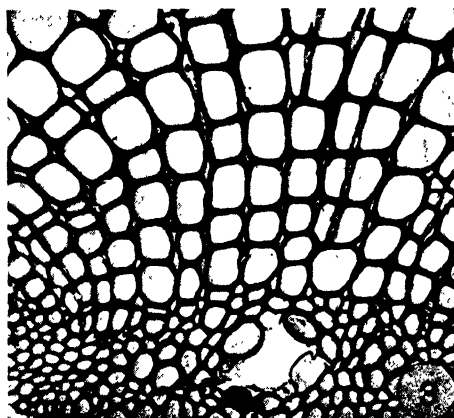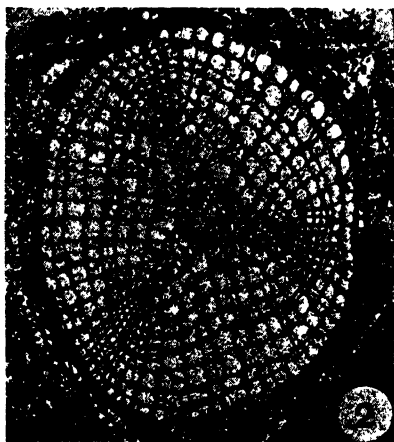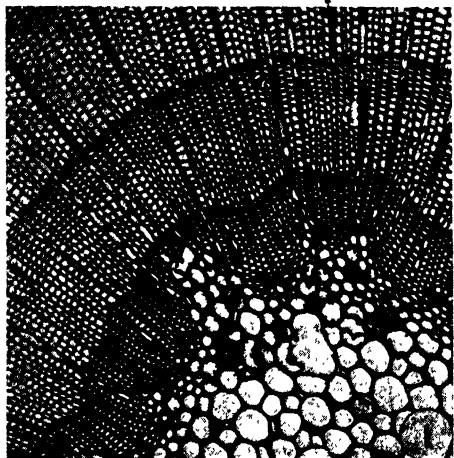
in the earlier-formed portions of the secondary body, particularly in the root, the segmentation of an entire fusiform initial may give rise to a vertical series of ray initials. From this vertical series several rays of two or more cells can be formed very near the place of origin by the vertical approximation of the component initials. Usually, however, when segmentation occurs, the individual ray initials continue radial elongation and periclinal divisions independently of the surrounding tissue. Subsequent transverse anticlinal divisions of the initials may bring two or more low rays which are increasing in height into vertical proximity, which results in the formation of a high uniseriate ray. The processes involved in the increase and decrease in height of rays will be dealt with later.

The four methods of origin of ray initials in the secondary body differ somewhat in cytological details. Each type will be discussed separately.

(1) Ray origin by division at the upper or lower end of a fusiform initial is the predominating method in all conifers. It is this type that both Schmidt and Klinken described as the apparent means of formation of new ray tissue in the cambium of conifers. Inasmuch as they were concerned only with older stem tissues it is not surprising that their conclusions accord with other evidence. Any truly radial section of coniferous wood reveals this process. The details of the cellular changes involved are frequently obscured by the apical growth changes which occur in the xylem during differentiation. Because of this difficulty Schmidt and Klinken failed to offer proof of their conclusions.

In this study definite evidence was obtained that cell divisions actually occur at or near the apex of cambial fusiform initials in the formation of new ray initials. The use of serial tangential sections of the phloem avoided the confusing changes that characterize differentiation in the xylem. One-celled rays were traced outward in successively older regions of the phloem until their exact means of origin was determined. In most of the sequences that could be completely traced, the divisions occurred at or near the tips of fusiform initials.

In the cambium illustrated in figure 7 the division that gave rise to a new ray initial occurred shortly after an anticlinal division of the fusiform initial. Such cell divisions in the ends of fusiform initials may involve the entire apex of the initial, in which case the cell is truncated and thereby decreased in length, or they may occur at varying distances from the end. The two positions of newly-formed walls are shown in figure 17. In 17b the cambial initial is not decreased in length since the cell plate twice intersects the same side-wall of the parent cell, whereas in 17a, the entire end of the fusiform initial is involved in ray initial formation, so that the initial is decreased in length by the height of the ray initial formed. These types of
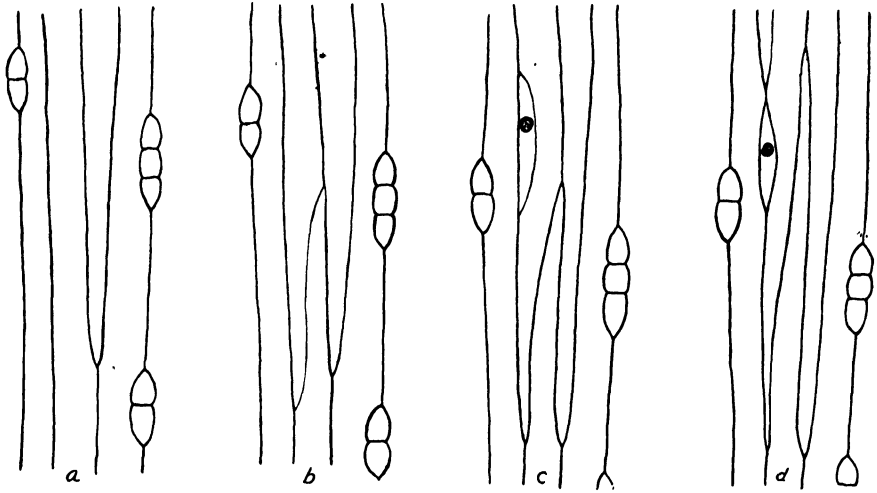
Fig. 7. *Cedrus libanitica.* Serial tangential sections of phloem, showing the origin of ray initials in the cambium; in *a* the condition in the cambium before anticlinal division of fusiform initial; in *b* anticlinal division of fusiform initial; in *c* the origin of a ray initial at the side of a fusiform initial. *d* illustrates further change in size and shape of ray and fusiform initials during successive divisons in the cambium. ×180.

end-wall formation are due to varying orientation of the phragmoplasts during cytokinesis.

The validity of this relation between the position of the cell plate and the size of the fusiform initial is borne out by a careful study of radial sections of the xylem. Figures 14 and 15 illustrate ray origins from the ends of fusiform initials. In figure 14 the formation of a ray cell did not decrease the length of the parent initial, as is indicated by the increasing length of successive cells in the row of tracheids. In figure 15, on the other hand, there is a reduction in length of the tracheary daughter cells equivalent to the height of the newly-formed ray cell.

The origin of ray initials at the ends of fusiform initials is therefore of two types: (a) the cell plate twice intersects the same side-wall of the parent fusiform initial; (b) the cell plate cuts off the end of the fusiform initial.

The cytology of such a series of cellular changes presents certain interesting problems; for example, that of the behavior of the nucleus. The nucleus ordinarily is central in the cell during the frequent periclinal divisions by which increase in thickness of xylem and phloem is accomplished. However, it is clear that when anticlinal or pseudotransverse divisions occur in cells of the size and shape of fusiform initials very extensive nuclear migrations must occur after formation of the cell plate. The two nuclei that result from the division migrate to the central regions of the

daughter cells before further periclinal divisions occur. Moreover, if the ray initial originates as is indicated in the series of diagrams in figure 7, still further nuclear movements take place. In this case the daughter nucleus of the upper, newly-formed fusiform initial migrated from its recently assumed central position, divided near the end of the cell and returned to the center before the succeeding periclinal division.

In the formation of a ray initial in this manner there is a complex series of nuclear movements indicated by the following sequence:

(a) an original central position of the nucleus in a free fusiform initial;

(b) an anticlinal cell division, followed by migration of the daughter nuclei to the centers of the resulting cells;

(c) a periclinal division of the two fusiform initials, with both nuclei remaining in a central position;

(d) a migration of the nucleus of one fusiform initial to the apical region;

(e) the formation by cell division of a ray initial near the region of the preceding anticlinal division;

(f) a remigration of the nucleus of the fusiform initial to the center of the cell;

(g) the normal periclinal division of both ray and fusiform initials.

The actual time involved in these nuclear migrations is apparently very brief. In hundreds of sections of white pine cambium, killed and fixed at the time of greatest rapidity of cell division, no division figures were seen in the ends of fusiform initials. However, several nuclei were observed in the apices of initials. Figure 13 shows the nucleus of a fusiform initial of *Pinus Strobus* L. near the extreme end of the cell. It is evident that remigration of the nucleus occurs very quickly after the formation of the ray initial. This inference is substantiated by the fact that the nucleus is in the center of the cell during each periclinal division of the initial.

(2) Origin from the side of fusiform initials is another frequent source of ray initials in coniferous cambia. The cell division that gives rise to such

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Explanation of Figures 8–12

Fig. 8. *Taxus baccata* L. Fusion of two rays by the loss of an intervening fusiform initial. Redrawn from Klinken.

Fig. 9. *Taxus baccata*. Splitting of ray by apical growth of fusiform initial. Redrawn from Klinken.

Fig. 10. Diagram of the relative size and shape of erect cell initials and ray initials in *Pinus Strobus; a*, the tangential, and *b*, the radial aspect.

Fig. 11. *Pinus resinosa* Aiton. Radial longitudinal section of xylem showing the origin of the ray from a cambial initial that previously functioned in the formation of erect phloem cells. Redrawn from Chrysler. ×225.

Fig. 12. *Cedrus libanitica*. Radial longitudinal section, showing origin of a ray and transition from vertically to radially elongated ray cells. Note amoeboid appearance of ray cells. ×150.

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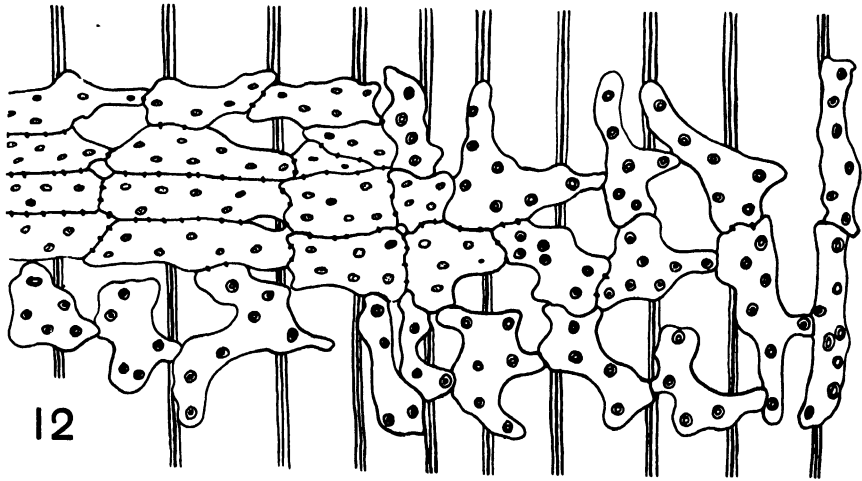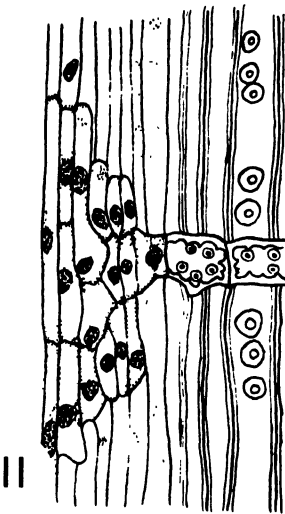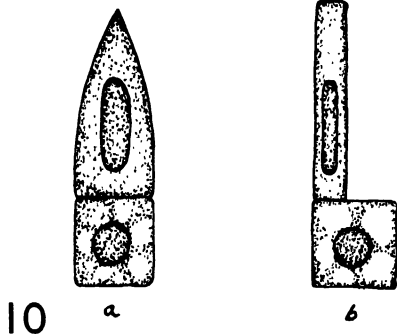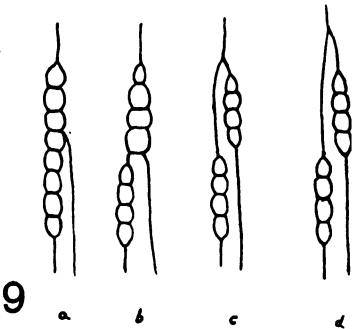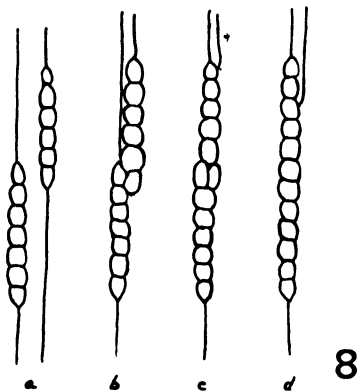
ray initials occurs at or near the central region of the fusiform initial. From the standpoint of its cytology it is therefore merely a modification of the first type. All degrees of transition exist between these two positions of ray cell formation. Figure 21 is a photograph of the cambium of *Pinus Strobus* showing the formation of a ray initial laterally from the parent fusiform initial. The figure also illustrates the vertically elongated shape of newly-formed ray initials. This vertical elongation of the first formed derivatives of such initials (Fig. 23) makes it possible to recognize ray origins in radial longitudinal sections of the xylem. The immediately succeeding ray cell may be of a very different shape, with its long axis oriented in the radial plane, as shown in figures 14 and 23. In the Taxaceae, Cupressaceae, and Araucariaceae, the transition from the erect, newly formed ray cell to the succeeding radially elongated cell may be very

Fig. 13. *Pinus Strobus* L. Tangential longitudinal section of cambium, showing position of nucleus in apex of fusiform initial. ×280.

abrupt, with complete contiguity between the two cells, as is shown in figure 15. In the Pinaceae and many of the Taxodiaceae, on the other hand, the newly formed cells are frequently isolated, and considerable time may elapse during successive divisions before a radial continuity of the cells is brought about. Compare figures 23 and 24.

(3) The two methods of ray origin discussed above account for the formation of most new rays in the older (later-formed) secondary xylem of coniferous stems and roots. As the growth rate slows with increasing age, there is a tendency towards the restriction of ray origins to single cells derived from the ends or sides of fusiform initials. However, in young, rapidly growing stems, and more particularly in roots, there is a somewhat different mechanism involved in the formation of ray tissue, the segmentation of fusiform initials. This term as used here connotes a series of transverse divisions in a fusiform initial which result in the formation of a vertical series of cells. Whether an entire fusiform initial is converted into ray initials is extremely difficult to ascertain, since the portion of the fusiform initial which may fail to form ray initials is lost from the cambium. In most of the sections that afforded critical evidence it was found that the number of individual rays that originated by the segmentation of a fusiform initial was always less than would be expected from a cell of such dimensions. In other words, in this process of septation a portion of the segmented initial fails to divide periclinally. This portion is either differentiated as a xylem element or is pushed out of the cambium by the surrounding fusiform initials.

In the early-formed secondary xylem of coniferous roots, however, the segmentation of an entire fusiform initial into ray initials is not infrequent. Such complete transformations are rare or absent in corresponding regions of the stem. It is chiefly this difference in cambial behavior which maintains the greater abundance of ray tissue in the root than in the stem.

In general, segmentation of a cambial initial gives rise to a series of one-celled rays at varying distances from one another. The separation of these originally contiguous cells is brought about in the same manner as the transition from primary to secondary ray tissue. There is a shift in the orientation of the long axis of the cell, and almost invariably a tendency for each cell to separate from those above and below. Vertical fusion of these separate one-celled rays may occur subsequently, but it should be emphasized that high, many-celled rays in the conifers do not originate as such in the cambium but always result from a series of ontogenetic changes.

Segmentation of fusiform initials to form ray initials is not restricted to the younger portions of either root or stem, but may occur, though much less frequently, in the older wood. This is particularly true in those species which normally have diffuse wood parenchyma.

(4) The fourth means of origin of ray tissue is the derivation of ray initials from radial plates. The term radial plate has been used by Chrysler (1913) to designate certain radially arranged sheets of parenchymatous tissue characteristic of the phloem of Pinaceae. The significance and distribution of radial plates are a problem separate from that dealt with in this study, although certain histological details of the plates will be discussed in more detail later. The cambial initials that give rise to the plates are derived from fusiform initials by the same cytological processes involved in the origin of ray initials. These radial plate initials differ from the ordinary ray initials in that they remain erect, and give off chiefly phloem derivatives. In general, the radial plate initials are quickly lost from the cambium if they are not in close proximity to the marginal initials of pre-existing rays. With increase in extent of the phloem, therefore, the plates frequently become recognizable as distinct sheets of parenchymatous cells, often completely dissociated from the phloem rays. However, the radial plate initials that border upon or are in proximity with the marginal initials of a ray continue meristematic activity indefinitely, giving rise to a border of erect cells along the margin of the ray. Chrysler (1913) first pointed this out and concluded that it was due to the localized activity of the initials that give rise to a radial group which was in vertical contact with a ray. Chrysler showed further that in radial plate initials dissociated from rays cambial activity may be localized in the median region of the group with the resulting origin of one or more one-celled rays in the xylem. This process takes place by xylem-forming divisions of the radial plate initials in the cambium.

It is of interest to note that this origin of ray tissue cannot be explained by a study of serial tangential or of radial sections of the xylem only. The ray initial, when it first gives rise to a xylem derivative, has already functioned for a varying length of time as an erect cell initial of a radial plate (Fig. 11); hence its first xylem derivative has not the same spatial or cellular relation to the surrounding tracheary elements as the original ray initial had when it was formed in the cambium.

In general there is a strong tendency throughout the Coniferae to restrict the formation of new ray tissue to a single-celled origin in the cambium. These newly formed single ray initials are elongated to varying degrees in the vertical plane. Their shape and orientation are usually in striking contrast to those of the subsequently formed radially elongated or procumbent ray cells. The ray initials originate by divisions in the fusiform initials, never from differentiating tracheids as implied by Thompson, nor from the ends of sieve tubes as noted by Chrysler (1913). Frequently the first xylem derivatives of newly formed ray initials are tracheary rather than parenchymatous (Thompson, 1910; Bannan, 1934). The relative

frequency of the two types is variable, however, so that no great importance can be attached to the occasional occurrence of ray tracheids at or near the point of origin of the ray.

Ray Ontogeny in the Secondary Body

Klinken analyzed in detail the development of the xylem rays in the secondary wood of *Taxus baccata*. His results apply, with minor differences in detail, to all groups of the conifers, particularly to those in which the radial plates are absent or poorly developed. By means of serial tangential sections, Klinken found that individual rays during their development tend to acquire a fairly constant height, in terms of cell number. That is, low rays increase in height, while high rays decrease in height. The two processes operate independently. The present study corroborates Klinken's results, although the presence of radial plates greatly complicates the ontogenetic stages in the Pinaceae and to a lesser degree in the Cupressaceae and Taxodiaceae. Since the two processes involved in ray ontogeny are antithetic they will be considered separately.

(1) *Increase in Height of Rays.*—Increase in height of rays is effected most frequently by simple transverse anticlinal division of the ray initial in the cambium. In this way two ray initials are formed from one. In isolated ray initials this frequently occurs shortly after their formation in the cambium, as shown by figures 5 and 14. In rays that have already attained a height of four or more cells, the transverse anticlinal divisions are restricted to the margins of the ray. In the Coniferae there are neither vertical nor transverse anticlinal divisions of the initials in the center of the ray, such as so frequently characterize ray development in the dicotyledons.[1]

Although they are frequent, the total effect of transverse anticlinal divisions of marginal ray initials is not great enough to cause the formation of the very high rays found to a varying extent in nearly all coniferous woods. This is more apparent when it is considered that the transverse anticlinal divisions are not only restricted to the marginal initials of the ray, but are less frequent as the ray increases in height. It is true that in the root wood of Pinaceae, successive transverse anticlinal divisions of the marginal ray initials may give rise to sheets of ray tissue of considerable vertical extent. However, the very high rays of both root and stem arise in the Pinaceae as in other Coniferae by an entirely different process, ray fusion.

The fusion of adjacent rays was observed by Kny and later by Klinken in his detailed study of ray development in *Taxus baccata*. Klinken found that rays separated by tracheidal elements frequently came together by

[1] Except in abnormal cases and the very old wood of *Sequoia*.

the loss from the cambium of the intervening fusiform initials (Fig. 8). He found further that if the two rays overlapped after fusion the biseriate portion of the resulting ray became uniseriate by a loss of the ray initials on one side of the biseriate portion (Fig. 8). The new ray that resulted from this lateral fusion was therefore always uniseriate and equal in height to the total vertical extent of the two pre-existing rays. Bizarre as this seems to be, the loss of fusiform initials is rather common in coniferous cambia. Its frequency is evidenced not only by observed ray fusion but also by the following considerations. The high rays not only fail to increase their height extensively by anticlinal division of the marginal initials, but instead frequently tend to decrease in height by a loss of the initials from the margins or central portions. In other words, the very high ray is only a temporary phase of the development of ray tissue. Hence the continued formation of high rays depends on a recurrent loss of fusiform initials from the cambium.

In the Pinaceae, and to a lesser extent in the Taxodiaceae and some genera of the Cupressaceae, the formation of high rays in the xylem depends on another peculiarity of development, the meristematic activity of the initials that give rise to the radial plates. Certain initials in the radial groups, chiefly those associated with the margins of the rays, may give rise to xylem derivatives which are marginal on the ray. Two rays closely approximated vertically and not separated by fusiform initials often fuse by the meristematic activity of such radial plate initials on their margins.

In general, the marginal xylem ray cells formed by radial plate initials are distinct from the other cells of the ray. Whether they are parenchymatous or tracheary, erect or radially elongated, depends on the species, but all marginal ray tracheids and marginal xylem ray parenchyma cells of coniferous woods are derived from initials which at one time were part of radial plate tissue. Since the initials that give rise to radial plates originate in the cambium by the same sequence of cytological changes which characterize the origin of ray initials, it is not surprising that transitions occur between the typically vertically elongated or erect initials which form plate cells and the characteristic nearly isodiametric initials of the ray proper. There are, however, certain other histological differences between the two types of initials, as well as their derivatives, which will be considered below.

Radial plate initials that join two vertically adjacent rays are frequently very high and commonly give rise to xylem cells of very irregular shape. The height of these cells depends on that of the initials from which they were formed, and is not, as Thompson suggested, indicative of a stage in the transition of tracheids to ray tracheids. Sometimes the erect initials that bring about a fusion of rays become continually shorter and assume

the size and shape of the ordinary initials of the two rays. This is usually accompanied by anticlinal divisions in the erect initials, and often by a change in the xylem derivatives of the latter from the tracheary to the parenchymatous type, which completes the fusion of the rays. In those Pinaceae in which ray tracheids are abundant, such as *Pinus* and *Larix*, there is seldom a change from the tracheary to the parenchymatous type. It is common, therefore, to find in these genera rays with ray tracheids not only marginal but also intervening in the central portions. Such rays commonly arise either by the lateral fusion of two rays already possessing marginal ray tracheids, or by the vertical fusion of two or more rays through the meristematic activity of erect cell initials adjacent to them in the cambium.

Vertical fusion of two very closely approximated rays may occur by two other means, both of which take place irrespective of radial plates and hence may be found in all conifers. Occasionally in radial longitudinal sections two rays that have continued independently of each other for some distance suddenly fuse by the vertical expansion of the adjacent marginal cells. Rays so fused often separate shortly, and may remain separate or fuse again.

It might be thought that this is merely the appearance in radial section of the effect of the loss of a fusiform initial that separates two rays both laterally and vertically adjacent. However, the sequence of the tracheids in the radial rows, as well as the fact that a subsequent separation may occur after fusion, indicates that this is not so. There is an actual approach and adhesion of the plastic cell walls of the ray initials in the cambium.

The last mechanism whereby vertical fusion of rays may take place is the occurrence of transverse anticlinal divisions in the marginal initials of two vertically adjacent rays. The increase in height brought about by the addition of new cells at the margins brings the two rays into contact with each other and results in the formation of a high ray.

(2) *Decrease in Height of Rays.*—Decrease in height of rays was accurately described by Klinken, who found that two mechanisms are involved. It may occur by the loss of ray initials from the cambium, or by the splitting of one high ray in the cambium into two smaller rays.

Except in genera in which extensive reduction of ray tissue is indicated by predominantly low rays, the loss of actively dividing ray initials from the cambium is comparatively rare. When it occurs, the initial may be lost either from the central region of the ray or from the margin. Figure 18 shows the loss of an initial from the central portion of a ray of *Taxus baccata*. The drawing was made from a photograph of a section that included phloem, cambium and xylem. On the extreme right is the last xylem derivative of the initial which has been "lost" from the cam-

bium, while on the left the "initial" may be seen fully differentiated into a phloem ray cell.

The decrease in height of rays by splitting depends on the rate and extent of elongation of fusiform initials in the cambium. As shown by Bailey (1923) the increase in girth of coniferous cambia is accomplished chiefly by anticlinal or pseudotransverse divisions in the fusiform initials. The two daughter initials that result from this division elongate until they are as long as the initial from which they were formed. Elongation is restricted to the cell apices, which penetrate the intercellular substance between the surrounding initials. The actual separation of the large ray into smaller units is caused by the intrusion of the apex of the fusiform initial into the intercellular substance between the ray initials (Fig. 9). The apices of the fusiform initial and of its xylem daughter cells continually elongate during successive divisions and bring about a permanent separation of the two portions of the ray. It is apparent that the split must occur in the cambium and not in the daughter cells of the xylem, since changes in the latter during differentiation would not affect cellular relations of the cambial initials.

From the mechanics of ray splitting by the apical growth of fusiform initials it follows that high rays undergo separation into smaller units more frequently and more readily than do low rays. The purely statistical chances for a cleavage in the ray increase with the height of the ray. Therefore, the reduction in ray height by this means is a chance phenomenon, which tends towards the elimination or reduction of very high rays.

These theoretical considerations are borne out by observation. In radial longitudinal sections of coniferous xylem it is chiefly the higher rays that are split; only occasionally is a four- or five-celled ray divided.

Explanation of Figures 14–18

Fig. 14. *Ginkgo biloba* L.. Radial longitudinal section of stem, showing the relation of ray origin to the end of a tracheid, and indicating the origin of the ray initial from the end of a fusiform intial. Note sudden transition in shape between first-formed (A) and succeeding ray cells. ×210.

Fig. 15. *Amentotaxus argotaenia* (Hance) Pilger. Radial longitudinal section of stem, showing the origin of a ray in relation to tracheids. The ray initial was formed at the apex of the fusiform initial whose xylem derivatives are indicated (A and B). Contrast with figure 14. ×210.

Fig. 16. Diagram of the origin of erect cell initials from fusiform initials. *a*, origin at the side of initial; *b*, from the end of initial. The size of erect cell initials in proportion to fusiform initials is exaggerated.

Fig. 17. Diagram of two types of end origin of ray initials from fusiform initials. *a*, the entire end of the fusiform initial is involved in ray initial formation; *b*, only a lateral portion of the end.

Fig. 18. *Taxus baccata*. Radial longitudinal section of xylem, cambium, and phloem, showing loss of ray initial from cambium. Note the correspondence of cells on both sides of the cambium (A and A'). ×210.
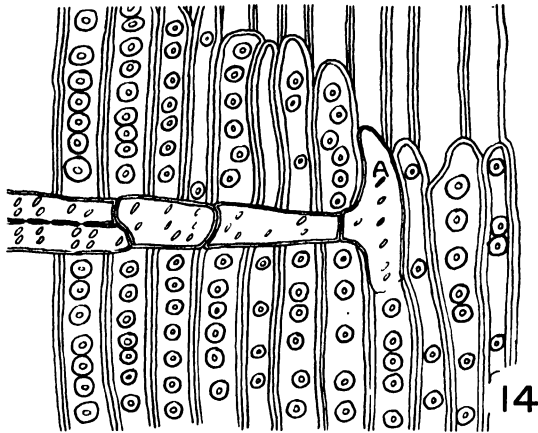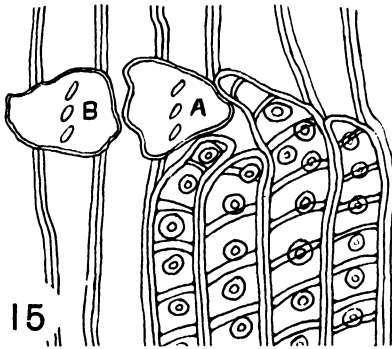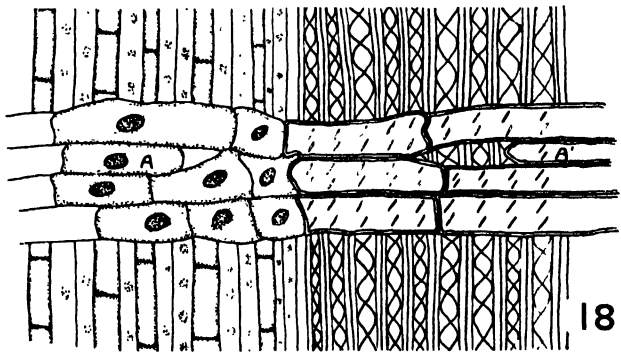
Radial Plates and Erect Cells

It was pointed out above that the radial plates are produced by initials whose origin in the cambium follows a somewhat modified series of cytological changes similar to those involved in the formation of ordinary ray initials. Apparently the plate initials originate most frequently by a division at the side of a fusiform initial. The wall formed in this division is long and intersects at its opposite ends the same radial side wall of the fusiform initial. The large vertically elongated cell so formed gives rise to a strand of smaller upright or erect cells by a series of transverse divisions. Figure 16a shows the first stage in the formation of a radial plate, before the occurrence of transverse anticlinal divisions. The plate initials may also originate at the ends of fusiform initials, as is shown in figure 16b. Occasionally the large initial formed by the original division in the fusiform initial fails to divide transversely, so that a short fusiform initial is produced. This is much higher than the normal erect cell initials, though otherwise similar. Such short initials may give rise on the xylem side to the short tracheids occasionally found in the wood of *Pinus, Picea,* and *Larix.*
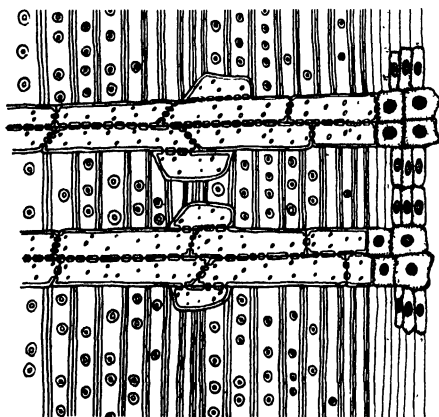
Fig. 19. *Abies balsamea* (L.) Mill. Radial longitudinal section of xylem, showing the relation of erect cell initials to marginal xylem ray cells. The xylem-forming divisions of the erect cell initials are less frequent than those of the ray initials. ×140.

After their formation, the radial plate initials divide for a short period, after which their meristematic activity dwindles. However, in radial plate initials that border on the marginal initials of a ray meristematic activity may persist, with the production of a border of erect cells on the phloem side of the ray and of marginal tracheids or parenchyma on the xylem side. The xylem-forming divisions of the erect cell initials bordering on ray initials are often less frequent than the divisions of the normal ray and

fusiform initials, and the xylem daughter cells are therefore scattered along the margins of the ray. Figure 19 shows this condition, very commonly encountered in *Abies*, *Pseudolarix*, and *Keteleeria*. The phloem erect cells, on the other hand, are in a consecutive sequence, so as to form a continuous marginal border on the ray. It has been observed frequently (Strasburger, 1891; Chrysler, 1913; Thompson, 1910; and Bannan, 1936) that erect cells of the phloem rays are usually coterminous with marginal xylem ray cells. Since the two cell types are derived from the same initial it follows that they will be coterminous unless delayed division of the initial causes a separation of its xylem and phloem derivatives. The xylem cells produced by erect cell initials are either parenchymatous or tracheary. Hence, both marginal ray parenchyma and marginal ray tracheids may occur not only in the same species but in the same individual ray. In general, in genera in which ray tracheids are abundant, the first xylem daughter cells of the radial plate or erect cell initials are tracheary. There may be a change from the tracheary to the parenchymatous cell type, though in *Pinus*, in which ray tracheids are very extensive, the erect cell initials give rise nearly exclusively to ray tracheids in the xylem. The difference between ray tracheids and marginal ray parenchyma is due entirely to the difference in secondary wall formation, since both have a similar origin in the cambium. Because of the close relationship between radial plates and marginal ray cells, the problem of ray ontogeny of conifers cannot be completely separated from the problem of the origin and nature of radial plates. Not only are the initials that give rise to the two tissues similar in origin, but there are also graded transitions between the two types of initials and their cambial derivatives. However, certain histological features of the radial plates or erect cells in the phloem necessitate a separate treatment, since they differentiate them from the remaining ray and phloem parenchyma.

It should be pointed out that the term "radial plate" therefore includes both the erect cells of a ray and the radial sheets of parenchymatous tissue in the phloem, whether or not these are associated with phloem rays.

A distinction between erect and procumbent phloem ray cells was made by Strasburger, who pointed out certain similarities between the former and sieve tubes. He observed that the cells on the margins of the rays in the phloem of various conifers are upright, completely lack starch, possess well-developed sieve areas, and tend to lose their cell contents contemporaneously with surrounding sieve tubes. Because of the absence of starch, the concomitantly greater "density" of the cytoplasm, and the presence of conspicuous protoplasmic connection with the sieve tubes, Strasburger designated these erect marginal cells *eiweisshaltige Zellen*. This term has been translated into English as "albuminous cells," which

expression is therefore synonymous with erect cells. In recent years the former has been more widely used; its uncritical acceptance has been unfortunate. "Albuminous" implies a fundamental protoplasmic difference between the erect marginal ray cells and the procumbent ray cells of the phloem, a difference not yet demonstrated by micro-chemical or optical means. There seems little justification for retaining a term of such definite and restrictive meaning when the basis for its usage has not been presented. There is considerable evidence that the absence of starch is not definitive of "albuminous cells." The inadequacy of this character has been noted by Chrysler (1913). My observations support the view that the presence or absence of starch is of no great importance in defining the morphological or physiological significance of erect phloem ray cells. Starch grains, though in somewhat smaller quantities than in the procumbent ray cells, were found in the erect cells of *Abies*, *Pseudolarix*, and *Pinus*, and would probably be found in the remaining Pinaceae if suitable material were examined.

In tangential sections of both the phloem and cambium of Pinaceae, stained in Heidenhain's haematoxylin or aniline blue, the erect cells are very frequently distinguished from the other cells of the ray by the apparent greater intensity of their staining (Figs. 20, 22). This difference has been attributed to a greater density of the protoplasm concomitant with the albuminous nature of the cells. However, an analysis of the factor that might be responsible for the apparent staining difference indicates that the cause is to be found in the physical rather than in the chemical properties of the cells. The orientation of the long axis of the erect cell is vertical rather than horizontal. This factor and the very small radial dimension of the cell make it very probable that even a thin tangential section will include entire cells, with both tangential walls and protoplasts intact. The procumbent ray cells, on the contrary, are radially elongated, and the chances are small that an intact cell will be included in sectioning. This difference of shape between erect cells and phloem ray cells is true

Explanation of Figures 20–24

Fig. 20. *Pinus Strobus.* Tangential longitudinal section of phloem, showing darkly staining cells of radial plate tissue; stained in aniline blue. ×250.

Fig. 21. *Pinus Strobus.* Tangential longitudinal section of cambium, showing origin of ray initial by division at side of fusiform cambial initial. ×650.

Fig. 22. *Pinus Strobus.* Tangential longitudinal section of cambium, showing erect cell initial persisting at margins of two rays; stained in Heidenhain's haematoxylin. ×310.

Fig. 23. *Cephalotaxus drupacea* Sieb. et Zucc. Radial longitudinal section of xylem, showing origin of ray. Note relation of the ray origin to the ends of tracheids. ×250.

Fig. 24. *Cunninghamia lanceolata* (Lamb.) Hook. Radial longitudinal section of xylem, showing an isolated, irregularly shaped ray tracheid. ×250.
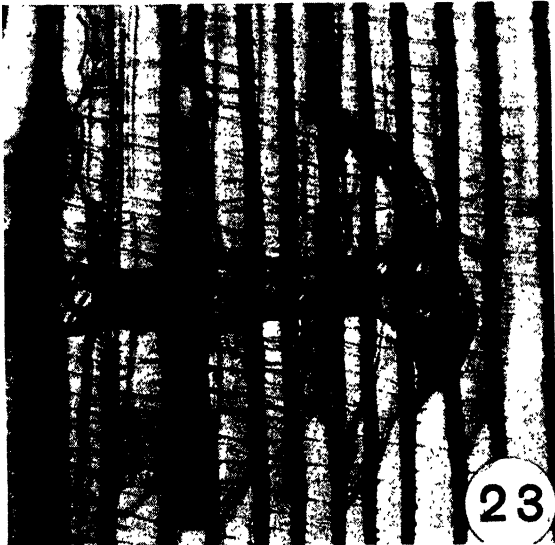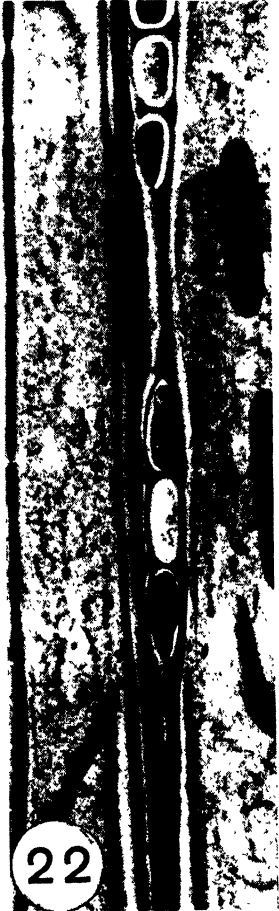
also of their respective cambial initials. Figure 10 shows diagrammatically the comparative size and shape of erect cell initials in the cambium of *Pinus Strobus;* figure 10*a* shows the tangential aspect, figure 10*b* the radial. In the mature phloem there is a still greater difference between the two types of daughter cells in their relative radial elongation, since erect cells undergo only slight changes in cell shape during differentiation, whereas ordinary phloem ray cells tend to elongate radially.

The difference in staining of these cells in tangential section is thus due primarily to the size and shape of the cells and not to a difference in the chemical nature of their protoplasts. This conclusion is substantiated by the fact that in radial sections the two cell types show identical reactions in both color and intensity of stain.

In general, the only morphological feature of erect cells that offers any basis for the term "albuminous" is the presence of sieve areas and protoplasmic connection with the sieve tubes. The erect cells in the phloem are apparently physiologically related to the sieve tubes, since they pass through similar ontogenetic stages, and lose their contents and develop callus at the same time as the sieve tubes.

That erect cells are found to a varying extent throughout the Coniferae indicates that among living genera there is a series of evolutionary stages in the development of this tissue. In the Araucariaceae, Taxaceae, and Cephalotaxaceae, in which erect cells are absent or very scantily developed, there are no organized radial plates of tissue in the phloem, and xylem ray tracheids are nearly if not completely absent except when associated with ray origins. In the Cupressaceae and Taxodiaceae erect cells are not infrequent, and radial plate initials of brief duration in the cambium are occasionally present. However, there is no extensive development of marginal xylem ray tracheids or parenchyma. In the Pinaceae, on the other hand, the tendency to form erect cells is strong and results in the formation of extensive plates of parenchymatous tissue in the phloem (Figs. 20, 22). Correlated with the increasing tendency towards the formation of radial plates and the concomitant erect cells of the rays is the increasing frequency of ray tracheids or marginal ray parenchyma in the xylem. Ontogenetically also the erect phloem cells appear first in the development of the secondary body before any xylem derivatives are formed by the erect cell initials (if they are ever formed).

The cytological complexity of the formation of erect cells and their apparent modification of function so as to be related to sieve tubes make it appear that the development of radial plates and erect cells is a phylogenetic line of specialization which culminates in the Pinaceae, more specifically in *Pinus.* That the development of ray tracheids is entirely

dependent upon the activity of the radial plate initials is additional evidence that ray tracheids represent an anatomic specialization.

The detailed histological problems associated with the ontogeny and the phylogenetic significance of radial plates are introduced here only because they are closely related to certain aspects of ray origin and ontogeny in the Coniferae.

SUMMARY

A review of previous research on the origin and development of ray tissue in the Coniferae reveals no comprehensive treatment of the problem. Fundamental cytological details have not been closely examined.

In the first-formed secondary xylem of coniferous stems most rays extend from the interfascicular segments of the stele. In the stem the rays are very low at the beginning of secondary growth; in the root they are considerably higher. This fundamental difference in height at the origin accounts, in part, for the greater abundance of ray tissue in the root than in the stem.

A careful study of coniferous cambium and phloem shows that the ontogenetic origin of ray tissue is a highly complex process, frequently involving extensive nuclear migrations in the fusiform initials.

In the secondary body of the Coniferae the majority of new rays are formed by initials which originate at the apex or sides of fusiform initials. The ray initials originate most commonly as isolated cells not associated in vertical series. The segmentation of fusiform initials also occurs.

The cambial initials which give rise to the so-called radial plates of the phloem of certain conifers may also enter into the formation of xylem and phloem rays.

Increase in the height of rays is accomplished in the cambium by increase in cell number per ray or by the fusion of two or more rays either laterally or vertically adjacent to each other. The lateral fusion of rays involves the loss from the cambium of intervening fusiform initials.

Decrease in the height of rays takes place by the loss of ray initials from the cambium and by the splitting of high rays into smaller units. Ray splitting occurs by the elongation of fusiform initials in the cambium.

Increase and decrease of ray height occur completely independently of each other, not only in adjacent rays but in the same ray.

The cambial initials that give rise to the radial plates of certain conifers originate by the same cytological mechanism as the ray initials. The morphological significance of radial plates is not considered, but their relation to ray ontogeny is briefly described.

It is recommended that the term "albuminous cell" be dropped, because of the lack of evidence to substantiate the meaning of the term.

The writer wishes to express his sincere appreciation to Professor I. W. Bailey for his active interest and aid in this work; and to Professor R. H. Wetmore for his advice and suggestions.

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Mention the BULLETIN

The Concept of the Genus [1]

I. History of the Generic Concept in Botany

HARLEY HARRIS BARTLETT

The concept of the genus must be as old as folk science itself. Certainly we find a nomenclature for plants and animals that is hardly different from modern scientific nomenclature among many peoples and in many languages.

It would be quite futile to speculate at too great length about how generic grouping had its beginnings, but there are two processes that must have been operative in ancient times just as they are today. (1) With enlarging experience, people make finer distinctions, and need different names for newly distinguished entities which have previously been called by the same original name. The original name becomes generic in its application; variously qualified it provides the basis for specific names. Thus genera are set up by analysis. (2) As language becomes cumbersomely rich in separate names for closely similar things, there is a tendency toward grouping or classification under the same name on the basis of newly perceived similarities. Thus genera are set up by synthesis. Many kinds of grass are so similar that we can hardly believe that the concept "grass" was not more ancient than the distinction of particular kinds. Here we have a hypothetical instance of the origin of a folk-science genus by analysis. On the contrary, the generic concept "fern" is a technical one, depending upon close observation, so when we find a people of relatively low culture, such as the Batak of Sumatra, defining extremely diverse plants as

[1] Papers presented at a Symposium of the Botanical Society of America, Systematic Section, and the American Society of Plant Taxonomists at Indianapolis, December 29, 1937.

[2] Papers from the Department of Botany of the University of Michigan, no. 713.

"fern" pretty much as the modern botanist does, on the basis of a relatively obscure characteristic, namely, the leaf-borne sporangia, we feel sure that a genus has been set up by synthesis of things superficially very unlike.

The grouping of distinguishable but similar kinds into genera seems always to have been a linguistic necessity if there was to be reasonable flexibility and precision in the nomenclature of plants and animals. The flexible and undefined categories genus and species ever sufficed for most purposes of folk science, and so we find by the analysis of common speech that only these two are indicated in the plant nomenclature of most languages.

The scientific concept of the genus is therefore not modern at all. It did not originate with Linnaeus or with his great predecessor, Tournefort. Rather, the nomenclatural reforms of both brought the Latin names of plants back into conformity with the usages of common speech, a conformity which had existed in science at the beginning of the sixteenth century but was gradually lost through the two centuries that intervened between the German Fathers of Botany and the great reformer, Linnaeus.

Complete scientific systematization of plants and animals has brought into recognition higher or more inclusive categories than the genus. Folk science had a vague need for these, and sometimes recognized their existence, as in instances that will later be briefly alluded to. Nevertheless, in speaking of the generic concept in folk botany as needing little change to become essentially the generic concept of modern science, I must of course guard myself by insisting that the inclusiveness or size of genera, now as in the past, is less a matter of science than of linguistic preference and convenience.

Classical botany was folk science. It did not progress far beyond the gathering together of folk beliefs and practical information. Theophrastus dealt almost entirely with cultivated plants, and Dioscorides with medicinal ones, and each systematized the knowledge or belief of his time with regard to the particular plants that interested him. Although they had no Dioscorides to record it, the illiterate barbarians of northern Europe probably had a folk science and terminology nearly as extensive and useful as that of Greece or Italy. Contemporaneously, an equivalent folk science would have been found in Egypt, in Ethiopia, in Palestine, in Persia, in Mesopotamia. There is, as a matter of fact, a modern interpretation of an old Babylonian herbal. China has its ancient knowledge of plants with a surviving literary record in a long series of printed Pênts'ao or herbals dating back at least to 1100, and based upon folk science hundreds or thousands of years older. China passed its learning on to Japan, where there was certainly already a native lore which was grafted upon the Chinese. India

early had systems of native medicine and associated plant lore which have come down to the present time partly by way of literature and partly by way of tradition. Anyone who delves into the beliefs of the peoples of the East Indies cannot fail to be impressed by the voluminous lore of plants, comparable in extent and value to that of the classical Greeks or Romans, and maintained by a nomenclature quite as scientific as the best in European botany during the time preceding Linnaeus. The New World had developed its own plant lore, an extensive body indeed in ancient Mexico, with its associated system of plant names and plant classification. Wherever we look into the matter, whatever the people or the language, we find naming and classification of plants, and almost invariably a more or less well-defined idea of the genus, as the smallest group that almost everyone might be expected to have the name for in his vocabulary. It might or might not be subdivided into species.

The idea that the generic concept is a characteristic of folk science will be found carefully developed in E. L. Greene's *Landmarks of Botanical History*. I have carried the development somewhat farther, anxious to show that the generic idea is concerned in its beginnings with the psychology of language, that those beginnings are lost in pre-history, and that we can only recover some conception of them by the consideration and comparative study of the plant names of people everywhere.

The tendency to group plants into named genera, so generally characteristic of human thought and language, reflects the fact that there are not enough different words in the living, current vocabulary of any language to supply each closely similar plant with a basically distinctive name. We, for example, apply the name oak to many different trees, but so long as we stay in our own proper north-temperate habitat, our generic feeling for the oaks is true and consistent. As a matter of fact, Greene has shown that the generic idea "oak," as held today, was really borrowed by scientific systematic botany from the folk science of the English pioneer settlers in temperate America, who extended the English folk concept of "oak" to cover the various widely different American oaks. In the eastern United States we distinguish white oak, burr oak, chestnut oak, live oak, scarlet oak, black oak, shingle oak and others, having a perfect binomial nomenclature for them in English, and, from the literary record, we may be sure that these designations owe nothing to scientific botany. They were in use in folk science before the botanists with their imperfect materials had anywhere nearly as good an idea of the oak species as the English colonists in the American woods.

In this instance the generic concept came from England, where there were only a couple of closely allied oaks, and was successfully applied to a multitude of popularly distinguished species. The botanists had long

labored under the difficulty of trying to recognize as many genera as there were Latin words for the few but exceedingly distinct oaks of Europe, namely, suber, ilex, cerris, robur, and quercus. We have here one example from folk science of the linguistic advantage of a large genus over several small genera. The generic concept is a variable thing in popular consciousness, as in science, but probably more uniformly and consistently applied in the folk science of most countries than in the systematic botany of the sixteenth and seventeenth centuries. We need have no doubt that ancient Latin and Greek folk botany, only imperfectly preserved in the literary record, were much more complete and perfect than the medieval "scientific" botany which in countries remote from the Mediterranean basin forced vaguely understood Greek and Latin nomenclature upon the plants of Germany and other parts of northern Europe. Likewise we may be sure that the folk science of unsophisticated peasants in almost any place in Europe, in any period of the Middle Ages, if it had ever been painstakingly and completely recorded, would have been better, from the standpoint of system, recognition of natural genera, and nomenclature, than the degenerated classical botany of the sophisticated at the same time.

Beginning with the great German botanists of the sixteenth century, the more the botanists broke away from the shackles of the completely decadent literary tradition, the more ready they were to make a beginning in good systematic botany by translating into Latin the names of plants that the common man knew, and knew not merely as species but also in groups, for which there were vernacular generic names. Reverting to the example drawn from our oaks, the folk botany of the American pioneer gave botany eventually not only such species concepts as those of *Quercus coccinea*, scarlet oak, *Quercus imbricaria*, shingle oak, and *Quercus tinctoria*, dyer's oak, but the generic concept implied by the adoption of these translated names. Many unnatural concepts of the late medieval botanists in time came to be corrected by adoption of popular concepts that were better than the quasi-scientific. To jump over several centuries in our argument, for the sake of driving the point home, it may be pointed out that Linnaeus, who followed folk botany in the matter of the oaks, followed pseudo-classical medieval tradition in disregarding it when he made the classical name Juglans do service for both the walnuts and the newly discovered hickories of the New World. It was not long after the time of Linnaeus that the popular generic conceptions of "hickory" and "walnut" superseded his earlier and unnatural forcing of the hickories into *Juglans*. The popular generic concepts of "sumac" and "poison-ivy" are now by way of prevailing over the impossibly inclusive *Rhus* that many scientists have held even down to the present. Although it would be absurd to force

the idea too far, it is clear that folk nomenclature may provide good indications not only for practical but for scientific generic grouping.

In whatever race or country we look for it, we find the classificatory instinct more or less strongly developed, and finding expression in the grouping of species into genera. There is everywhere a tendency to group similar species under generic names, and to name the species by using some linguistic device not unlike the binomial nomenclature of Linnaeus. There would seem to be a good psychological basis for binomial nomenclature. As many basically distinct words will be current in each vernacular as an intelligent speaker (or better, perhaps, the total of those persons of diversified experience and occupation who speak a vernacular) can attach ideas to. These basic plant names are not enough to go around. Therefore grouping into .genera is linguistically and psychologically inevitable, whether the grouping results from failure to see differences or from especially keen apprehension of similarities.

Recently I have been giving much attention to the climbing palms of the Malayan region. Since these plants are very different from each other in their utilities, it is natural that they should be critically systematized by the native peoples who live where they grow. Ordinarily they form, popularly, only a single genus, which may be called *rotang* (we get our English word "rattan" from this), or *hotang*, or *uwai*. Under the genus are arrayed the species, *hotang soga, hotang djorlang, hotang sumambu, hotang ahonir, hotang taritting, hotang pahoe* and many others, to cite only part of the names from a single place and dialect.[1] The distinctions are known to most of the people of the forest, and are based upon many of the same morphological features that would be utilized in classification by a trained botanist. Of all the plants called *hotang* (in the district of the east coast of Sumatra where I am best acquainted with people and flora) only one, *hotang da ursa,* is not a climbing palm, but it is *Flagellaria,* a climbing, monocotyledonous plant recognized by the natives as so different that *hotang da ursa* is itself treated as a genus. Whereas any of the climbing palms may be called simply hotang, the *Flagellaria* may not be. It must be called by its full name, *hotang da ursa.* Here we get an inking of how generic designations of more than one word arose in other languages.

In these names of the climbing palms we have a paradigm to illustrate the working of the human mind in arriving at a classification and nomenclature of plants. We see the interplay and balance between the limitations of vocabulary, on the one hand, and comprehension of differences among a multiplicity of interesting and useful natural objects, on the other. The number of basically independent words that can be sufficiently utilized to

[1] Pardembanan dialect (a sub-Toba dialect) of Asahan, Sumatra.

be retained in the vocabulary is so much more limited than the objects for which names are needed that a binomial system develops as a matter of course. Among the Batak the grouping of inconsequential things is very inclusive. For instance, *"duhut"* will do for a wide range of weeds or herbaceous plants, but scores or hundreds of kinds of *duhut* that are important enough so that they must be talked about have generic and specific names. *Pahu* will do as the generic name for almost any fern, but a great many species and a few restricted genera are recognized. Even such an aberrant thing as *Ceratopteris* is recognized as a fern. *Saio* is *Selaginella.* It is recognized that there are several closely similar kinds, but nobody bothers to give them names. (Until recently the botanists did not, either!) An inclusive generic name for almost all moss-like plants is *lumut.* Classification of *lumut* is hardly attempted, but the conspicuous *Leucobryum* has a generic name. The condition of moss nomenclature is after all not so very different from that in scientific systematic botany before Dillenius. As to plants in general, there is a partial classification, going to genera or species in hundreds of instances, but leaving many plants unclassified, regarding which all that the native botanist will say is that they are trees, herbs, vines, ferns, or mosses. Any very slender sedge is *si martihe-tihe,* "the one who passes for *tihe"* or "the tihe-like one" (*tihe* being a particular kind of sedge) and many other designations of this sort are very broadly but discriminatingly classificatory. Here we have an inkling of the family concept and a name which is linguistically a reflection of the same kind of thinking that gave us the botanical family names in current scientific use. But we are concerned with genera, and must not digress too far.

To repeat, the generic concept is so useful in classifying knowledge and has been so logically and extensively applied in various parts of the world, that to trace its history would be to trace the history of language and thought itself. All that we can profitably do by way of tracing the concept as it is reflected in scientific botanical nomenclature is to review the status of genera in works of some of the great botanists who preceded Linnaeus, to show that Linnaeus based his clear concepts of genera largely upon Tournefort and Plumier, and that his reform in nomenclature was a reversion to ancient simplicity of speech, and to point out that in the main the changes that have come about since Linnaeus have been to define genera as groups of species that do not seem to violate the conceptions of natural affinity by descent that were developed by Darwin.

Let us begin with the work of the first of the German Fathers, Brunfels, whose great herbal was first published in 1532. In discussing his work, I wish to make an important point clear at the outset, namely, that his generic names were generally but not always single words. During the

middle ages the language in common use for learned books was Latin. Latin has only a small store of original plant names and does not readily lend itself to the formation of new ones, as Greek does. In Latin, therefore, many genera had two-word names, and to name a species, by adding a qualifying term to the generic name, required the use of at least three words. Brunfels replaced some, but not all, of the confusing two-word Latin generic names by single words. He left, for instance, the two-word generic names *Sigillum Salomonis*, "Solomon's seal," and *Bursa Pastoris*, "shepherd's purse."

Even if Brunfels' genera are not always such, according to our modern evolutionary ideas of plant affinities, they often conform exactly to modern genera, or at least their species belong to the same family. Thus he had a mallow, which, being in his opinion the true *Malva* of the ancients, he called simply *Malva*, with no qualifying designation, whereas a second species he called *Malva equina*, "horse mallow." In the Latin edition of his herbal he gives a German nomenclature that corresponds exactly to the Latin names, namely, *Bappelen* and *Rossbappelen*. If, however, we turn to the German edition, the nomenclature is more in accord with Linnaean and modern usage. The true *Malva* is *Gaenssbappelen*, "goose-mallow," and the other is *Rossbappelen*, "horse-mallow." We have specific names made in a Teutonic way by compounding an adjective modifier with the generic name rather than in the Latin manner, which keeps the words separate, but the basic idea of qualifying a generic name to make a specific one is there. Brunfels has examples of both ways, in his German edition. We do not find complete consistency in Brunfels' work, but enough to show that he had the modern idea of the genus, as a group with morphological similarities, within which the species were grouped. Furthermore, he arrived at the more modern features of his work by turning German common names, of the sort just cited, into Latin. The result of necessity resembled the Linnaean binomial system if the generic name was only a single word, for then the addition of one qualifying term made a binomial specific name of quite modern aspect.

We find *Helleborus niger*, for example, and *Plantago major*, names which meant to Brunfels in the year 1532 just what they mean to us now. One of the most interesting points in connection with Brunfels' nomenclature is that it displays the generic concept quite as definitely in German as in Latin. A glance through the German edition brings to light such genera as *Seeblüm* for the water lilies, the species being two, the white and the yellow. They are separate genera in the eyes of modern botanists, but in German folk botany, as reflected by common names, they constituted a genus of two species. We find two primroses, *Geel Hymmelschlüssel* and *Weiss Hymmelschlüssel*, a perfectly good example of the generic concept

as well as of binomial nomenclature, and, a few pages farther on, *Edler Augentrost* and *Weisszer Augentrost*. Here, according to modern ideas, the genera are different but the family is the same. The important point is that it is quite as characteristic of folk botany as of modern systematic science to classify to the genus, which is more or less consciously thought of as the smallest grouping requiring a distinctive name. Within the genus, if the distinction of several kinds is necessary, a qualifying designation is used and the whole name becomes a binomial. If there is but one sort within a genus, no qualifying word is necessary, for the generic name is sufficient. Brunfels did not try to invent Latin names for plant genera that perhaps the ancients did not know. He was satisfied to call the little *Draba verna* of later botanists merely *Gaenssblum*, and Adanson, the radical in botanical nomenclature, who did not care whether nomenclature was Latin or not, took this German name as the valid scientific one for the genus, attributing it to Brunfels. For another plant that Brunfels found no name for, not even in German, he was content to say that the name was unknown. That was equivalent to recognizing its generic distinctness from the other plants in his herbal, even though he does not go to the length of naming it. It was the first published record of *Anemone nemorosa*. There is little evidence that Brunfels' botanical knowledge, aside from his efforts to identify most of his plants with those known to classical writers, was other than a very intelligent sifting of current folk botany. His definite attempts at classifying similar plants into genera. we may think of as expressing the natural tendency of Germanic thought and language. His recording of what appears to be genuine folk science represented an immense improvement over the debased travesty of classical botany which, constantly vitiated by gross error, superstition and fraud, had reached an unbelievably low level in some of the works of the type of the *Hortus Sanitatis*.

This glimpse at Brunfels' simple and practical generic ideas and terminology must suffice for his century. Unfortunately many of his successors continued in vain the process of trying to squeeze plants totally unknown into old genera, with the result that the simplicity and clarity of Brunfels' work soon disappeared. Scientific botany became more and more involved. The generic idea, so clear in most folk botany, became less so, and specific names, long and rambling ones, did not necessarily incorporate the generic name at all.

In 1623 the learned Caspar Bauhin published his *Pinax Theatri Botanici*, a work on which he spent forty laborious years. It was an index to all plants known up to his time, listing all the supposed synonymy. As the title indicates, it was but a prepublication of the index to a most ambitious work, the *Theatrum Botanicum*, of which Book I, treating

"grasses," was the only part that was complete at the time of his death, and which was actually published in 1658 by his son. There is also a *Prodromus Theatri Botanici*, published in 1620, including only preliminary descriptions of the undescribed species detected by Bauhin during his long botanical career. The three works together are an excellent source of information on the status of the generic concept at the beginning of the seventeenth century.

Bauhin's *Pinax* says that Dioscorides and Pliny made four genera of grasses, whereas later botanists made many. These later "genera," to take a couple at random, are such as the following: *Gramen caninum* (comprehending species that Linnaeus later put into *Triticum, Poa, Agrostis, Aira,* and *Cenchrus*) and *Gramen junceum et spicatum* (including Linnaean species of *Festuca, Aira, Juncus, Scirpus, Carex,* and *Triglochin*). Such genera are not so good, on the whole, as some of Bauhin's predecessors nearly a hundred years before would have made, and the generic concepts and nomenclature have become vastly complicated, but we must bear in mind that Bauhin was primarily indexing rather than reforming. Taking a typical case, that of *Cyperus*, he says that the species may be bitter, or they may be sweet (and edible). A bitter *Cyperus* may be either odorous or inodorous, and some part of it may be either round or long. So he divides *Cyperus* into five genera, with the polynomials *Cyperus rotundus odoratus, Cyperus rotundus inodorus, Cyperus longus inodorus,* and *Cyperus esculentus.* The assemblage as a whole includes a medley of types, Linnaean species of *Cyperus, Carex, Schoenus, Scirpus,* these all *Cyperaceae*, but with them also *Dorstenia* in the *Moraceae.* Obviously there was only a vague idea of any morphological criterion of a genus in Bauhin's mind. As to his nomenclature, there are many instances, perhaps a majority, in which the generic name is incorporated at the beginning into the name of the species, as for instance, most of the species of the genus *Gramen caninum*, two of which are *Gramen caninum, supinum minus,* and *Gramen caninum maritimum spicatum.* Another species of the same Bauhinian genus, however, is *Gramen murorum radice repente.* Here there is nothing in the name to indicate that the plant belongs to the genus *Gramen caninum.* Then there are many instances in which the name for a segregated genus is a condensation of the polynomial name of a species. Thus the two species of the genus *Cyperus esculentus* are *Cyperus rotundus esculentus angustifolius* and *Cyperus rotundus esculentus latifolius.*

The casual reader of Bauhin might too hastily conclude from the chapter headings that his real genera were not the groups, often with binomial and trinomial designations, which are divided into numbered species, but rather the larger categories with monomial designation that head the chapters. It is quite true that some of the genera do indeed have one-word

names, which are used also as chapter headings, but more often this is not so. For instance, Bauhin says that it is possible to reduce the orchids to the five genera which he calls (1) *Cynorchis*, including a subgenus (although he nowhere uses this term) *Cynorchis militaris*, (2) *Testiculus morionis*, which he immediately changes to *Orchis Morio*, (3) *Orchis foetida*, (4) *Orchis Serapias*, and (5) *Testiculus odoratus*. By the time he gets to the actual treatment of the fifth it appears as *Monorchis et Triorchis*. Aside from a few specific names that begin as we would expect with the generic name, we find some species under each whose long names give no clue to the genus under which they are placed. Thus under *Cynorchis* we find names beginning with *Orchis* and *Chamaeorchis;* under *Orchis Morio* are *Orchis flore nudi hominis effigiem repraesentans, mas* [*et foemina*] and *Orchis flore simiam referens;* under the genus *Orchis foetida* are species with names such as *Orchis odore hirci minor;* under *Orchis Serapias* no names begin thus; under *Monorchis et Triorchis* (treated, if we may judge by the numbering of the species, as a single genus) the specific names begin with *Orchis, Triorchis,* and *Chamaeorchis.*

In the work of Caspar Bauhin, therefore, the generic concept in botanical classification has become almost wholly divorced from language. The names of species need have nothing whatever to do with the genera to which the species belong. Not one of the phrase names which he retains or proposes for the species of *Curcuma* refers to the genus, and such as *Cyperi genus ex India* and *Crocum indicum proposuit Garcias, foliis milii majoribus: et Acosta, foliis Orchidis Serapiae dictae majoribus latioribusque,* give an altogether wrong indication of relationship, for a *Curcuma* can neither be a *Cyperus* nor a *Crocus* according to Bauhin's own classification. The name of a species by Bauhin's time has become something that need not indicate any genus and may even indicate a genus from which the species is excluded. A name is merely a name, not necessarily indicating generic affinity at all, and knowing where species belong has become merely a feat of memory. Truly simple generic grouping, as found in folk botany and reflected in language, had been lost, by the time of Bauhin's *Pinax,* in a maze of complexity and obscurity.

Matters did not greatly improve until drastic reforms were instituted by Tournefort about 1700. He restored the generic concept to simplicity and utility, and in conventional botanical history is the originator of genera. Of course he was not, but he certainly wrought a revolution in the jumbled botany that he found, turning chaos into order.

From the fact that Tournefort referred all the plants he knew to definite genera, it might be assumed that he had a well-defined underlying philosophy which enabled him to judge of what constituted a genus. He did have, and it is worth while to look into it, as he expounded it in the

famous *Isagoge in Rem Herbariam* which forms the introduction to his
Institutiones Rei Herbariae.

In the first place he shows that plants generally have roots, stems,
leaves, flowers, fruits, and seeds. There may be other parts, and at least
five may generally be considered in establishing a genus, for most plants
have that many, although some lack stems, some lack leaves, and some
lack flowers.

It is of no use, he says, to require close correspondence in as many as
five parts, in the species of a genus. There are not many genera with
species closely similar in roots, leaves, stems, flowers, and seeds. For
instance there are species of *Ranunculus* with tuberous roots, others with
fibrous, still others with grumose. The leaves of species in this same genus
resemble those of *Aconitum*, of grass, of rue, or of other plants, so one
cannot even demand correspondence in four parts.

Suppose correspondence in only one part is required. Then, he says,
we can't often arrive at good genera. The leaves alone would not do as a
criterion, for then to *Plantago* would have to be added all the plants with
leaves like those of plantain, such as the genus *Plantago aquatica*, and
the species *Ranunculus Plantaginis folio.* (Note that Tournefort keeps
binomial generic names, such as *Plantago aquatica* (now *Alisma*), *Lilium
Convallium* (now *Convallaria*), *Primula veris*, *Ruta muraria*, and a few
others.) Such a genus as *Plantago*, defined by leaves alone, would make
botanists laugh, Tournefort says. So would one based upon leaves like
those of *Aconitum*, for it would contain species of *Ranunculus, Geranium*,
and other genera. Flower form alone as a criterion would be no better, for
then, he observes, we would get a jumble of such things as *Cucurbita*,
Convolvulus, and *Campanula* in the same genus; nothing could be more
inept than such a composite. Likewise all the umbelliferous plants would
fall together, and an equal infelicity would result from dumping into one
genus all plants with papilionaceous flowers. Without laboring through
this part of his argument further we may state his conclusion that simi-
larity in two or three parts is all that is generally necessary.

Next he proceeds to show that roots and leaves together will not
suffice, nor roots and flowers, nor roots and fruits. However, similarity
in flowers and fruits will make the best criterion of a genus. This con-
clusion he proceeds to justify by saying that no one who looked at it in
flower and fruit could deny the name *Viola* to *Herba Trinitatis* of Fuchs.
The lack of conformity of its leaves and stems with those of *Viola vulgaris*
need not disturb us, any more than the conformity of the leaves of the
latter with *Asarum* would lead us to put it into the same genus with
Asarum. He depends upon conformity of flowers and fruit as the basis
for deciding what shall go into *Viola*, not leaves and stems, as Caspar

Bauhin does in the *Pinax*. "Good God," says he, "what a lot of things have come out of Africa in the last few years, in their foliage looking like *Malva, Alchemilla, Myrrh, Coriander, Aquilegia, Uva crispa*, and what not, but every one, by overwhelming consensus of botanical opinion, some sort of a Geranium!"

Tournefort grants that any rule of thumb may be too rigidly applied, however, and so he will make exceptions when he likes, in order to maintain such natural genera as *Castanea*, distinctive by what he calls its echinate calyx. So there will be genera of two orders of distinctness, which he will call genera of the first and second order, respectively. Of the first, defined by conformity of flowers and fruits, *Aconitum, Ranunculus, Rosa*, and *Viola* may serve as examples. Of the second order an example is *Bulbocastanum*, which differs only in its tuber, he says, from several genera of umbellifers. *Lilium* is maintained as distinct from *Tulipa* and *Corona Imperialis* by its "roots" being made up of scales, whereas the related genera have tunicated "roots." It is necessary to use characteristics derived from the position of the leaves to distinguish *Abies, Pinus*, and *Larix*. The tubular peduncle may suffice to separate *Dens Leonis* as a genus from *Hieracium*. As a final example, showing how far Tournefort was willing to go as a generic splitter, putting most moderns to shame, he says that sometimes the bark alone will do as a generic distinction, and he forthwith follows the ancients in setting up *Suber*, the cork oak, as generically distinct from *Ilex*, the live oak, and both as distinct from *Quercus!*

Tournefort expresses his opinion of his English contemporary, Morison, in an ungentle dig when he says that botany is being involved in a new fog by those who maintain that great genera are not to be split into smaller genera, but, rather, are to be divided into minor genera (subgenera). He cites Morison's polynomially designated subgenera of *Onobrychis*, namely, (1) *Onobrychis scilicet siliquis articulatis et asperis*, (2) *Onobrychis siliquis echinatis, cristatis et spicatis*, and (3) *Onobrychis siliquis echinatis, sed in capitulum congestis, Platani pilularum modo*. Of what use, he asks, is a name which has to do service for such diverse things? If his own definitions are too narrow, if, for instance, someone protests his definition of *Mandragora* on the ground that it requires that *Mandragora* have a monopetalous (i.e., gamopetalous) corolla, whereas there is a polypetalous *Mandragora*, he retorts that if such a polypetalous plant occurs there is no doubt that a new genus ought to be established, as he has often, in fact, established other new genera.

Tournefort's idea of the full names of species of plants is of no little interest. He says they are, after a fashion, definitions. First comes the name of the genus, and then the words expressing the distinctions of the

species. As we have seen, he carries on some old binomial generic names, but most names of genera are single words. He commends Caspar Bauhin for certain neat, brief, elegant, euphonious specific names that better invite to the study of plants than repel. Such are *Ranunculus nemorosus vel silvaticus, folio rotundo,* and *Ranunculus pratensis erectus, acris.* To be condemned, he says, are Morison and Breynius, whose specific names can hardly be uttered with one breath, and go two or three times across the printed page. One excellent reason for small genera, Tournefort says, is that the concept of the small genus comprehends more that is common to all the species, so that the names of the latter may be brief and sonorous. Better to propose new genera with audacity than to force species into places where they do not fit. If genera thus constituted for single species appear superfluous, don't worry about the matter; exploration will sooner or later turn up others.

Tournefort's ideas of genera were clearly pragmatic in the extreme. If new generic names would be conducive to understanding the nature and affinities of plants, he had no scruples about establishing them. Nevertheless he did not do so thoughtlessly or without good reason. His criteria were generally well considered, and few of his generic propositions failed, in the long run, to win the approval of Linnaeus and his successors.

Linnaeus wrote of Tournefort's contemporary, Father Plumier: "Standing forth among all travellers as the greatest, he discovered more than 900 new plants and referred all of them to definite genera. Would that we could have more Plumiers!" This was in reference to Plumier's *Nova Plantarum Americanarum Genera,* of 1703, and is almost the only reference to genera in the *Bibliotheca Botanica* of Linnaeus.

Linnaeus generally accepted the genera established by Tournefort and Plumier, and gave all genera single names, generally very well chosen. Apropos of names, in his quaint classification of botanical authors, he provided for "Nomenclatores Criciti," those who would teach how to construct generic and specific names correctly. Of these useful persons he admitted that none had yet written on this subject and then modestly listed himself as the only one there was! The sweeping reform of nomenclature which he later initiated more than justified his confidence in himself.

In Linnaeus' *Fundamenta Botanica* he laid down the fundamental principle that the genus and species are entities of nature. This conception has been denied by some, but it has clearly been and still is the basic belief of most systematic botanists. It guided Tournefort, then Linnaeus and his followers in grouping as genera those species of plants which seem most similar to one another. Close morphological similarity, in fact, was interpreted by Linnaeus as signifying real genetic relationship. He said himself that no true genus was other than a natural genus, and he even-

tually proposed a theory by which he brought into logical agreement two at first glance incompatible beliefs, that plants are all interrelated by descent, and that species were produced by special creation. I have elsewhere called attention to the curious doctrine, which Linnaeus made public relatively late in his career, according to which it was postulated that fundamentally distinct types, produced in the beginning by fiat, hybridized by miraculous intervention in an orderly manner in all possible combinations, which process was repeated by the primary hybrids and then again by the secondary, until the genera and the species were produced. He said that the morphological combinations, if botanists were keen enough to interpret them, would indicate the true genera. We must recognize that Linnaeus was a forerunner of Darwin to the extent that he believed in the relationship of species and genera by descent.

The constantly more refined methods of systematic botany and the doctrine of evolution, toward which Linnaeus groped, have given new meaning, since the publication of Darwin's epochal *Origin of Species*, to the Linnaean conception "entity of nature." Nevertheless, the majority of modern systematists, still mainly concerned, as Linnaeus was, with morphological criteria, continue to approve the generic concepts of Linnaeus. He himself, approving in general the concepts of Plumier and Tournefort, by the uniform application of the binomial system, restored to Latin botanical nomenclature the simplicity and intelligibility of common speech. Forgetting that large genera may be quite as truly "entities of nature" as small ones, some modern botanists are making far too fine generic segregations, in violation of evidence that too many basically different words for similar things cannot be borne in mind and fall into disuse, and that from a practical standpoint too many names and too many genera obscure rather than elucidate relationships. Just as we quite naturally accept the conclusion that the concept of genus in folk botany was often too broad, and had to be narrowed, so it is quite inevitable that botanists shall continue to accept new generic segregations whenever it appears from increased knowledge and new appraisal of characters that old genera are not natural entities. But that there is any need for a general change in the generic concept, from the standpoint of inclusiveness, we may deny. A large genus may be quite as "natural" as a small one, and from a practical and linguistic standpoint may be a far more useful concept.

ANN ARBOR, MICHIGAN

II. A Survey of Modern Opinion

EDGAR ANDERSON

When I was originally asked to speak on genera from the viewpoint
of cytogenetics, I replied that on this problem genetics could contribute
nothing and cytology very little. The chief technique of genetics is to
cross individuals and from the appearance of their progeny to make
inferences as to the germplasms of the two individuals. Very few genera
can be crossed and no exhaustive studies of the progeny have been made
in the few exceptional cases which were semi-fertile. The chief technique
of cytology is to make direct observations on the germplasm. This tech-
nique is obviously applicable to the study of generic differences but to
yield significant results it would have to be applied in various families of
the flowering plants and completely correlated with a taxonomic investiga-
tion of the same genera. Most of the cytological evidence compiled up
to the present time has been assembled by cytologists who were quite
innocent of any taxonomic training or insight and their data cannot
therefore be used for this purpose. The few projects which are now under
way (notably those of Babcock and Stebbins, 1937, on the Crepidinae and
Clausen and Keck, 1933, on the Madinae) are as yet too incomplete and
too restricted to permit effective generalizations.

Since, for the above reasons, it seemed to me that genera could not
be discussed from the viewpoint of cytogenetics, I asked to be allowed
to investigate them in another way. We may think of genera in two quite
different ways, (1) as biological units, that is as gross discontinuities in
organic nature, or (2) as cataloguing devices used by systematists. These
two concepts are overlapping. Such a distinction may even be unwelcome
to many biologists; it will, however, be a useful expedient in the following
discussion.

It seemed to me that if one could not yet investigate genera as they
may or may not exist in nature, he might at least learn something about
them *as they exist in the minds of taxonomists*. This I set out to do by
framing a questionnaire which would indicate something of the differences
of opinion among modern taxonomists. With the help of preliminary dis-
cussions with Dr. J. M. Greenman and Dr. C. L. Hitchcock (who are,
however, to be absolved from any responsibility) the following question-
naire was prepared and sent out to fifty taxonomists with whose work I
was personally acquainted. The list was representative and for reasons
which will be apparent below, was purposely devised to include monog-
raphers, plant geographers, and students of floristics.

For the symposium on Genera I am attempting to find the opinion of present day taxonomists. Will you, therefore, be kind enough to fill out the following questionnaire? A stamped, addressed envelope is enclosed for your reply. If you are unable to fill out the questionnaire will you at least indicate here your reason for not doing so?

( ) I am too busy. ( ) I feel the questions are trivial.
( ) I am out of sympathy with any such investigation.

Question No. I.

Which in your opinion is the more natural unit among the flowering plants, the genus or the species? (i.e., which of the two more often reflects an actual discontinuity in organic nature.)

( ) The genus is the more natural unit. ( ) The species is the more natural unit. ( ) I have no opinion on the subject. ( ) I think the question as phrased above is meaningless. ( ) I do not understand the question as phrased above.

Question No. II.

If genera are more clearly marked than species this may be due to either or both of two quite different processes: *A*. Genera may originate in the same way as species and achieve their greater distinctness by the disappearance of more intermediates. *B*. Genera may originate in a different way from species; i.e., it is conceivably possible that there are different forces which have operated in the origin of genera. If *"A"* has been the chief method by which genera have originated then the morphological differences between genera, though greater than those between species, should be the same *sort* of differences. If *"B"* has been the chief method then we might expect generic differences to be of another kind from specific differences. In the light of the above discussion will you indicate your opinion below? Check more than one space if you wish.

( ) Generic differences are of the same kind as specific differences though they may be greater. ( ) Generic differences are of a different kind from specific differences. ( ) I have no clear opinion on the subject. ( ) I do not think the statement has any meaning. ( ) In my opinion the statement is obscure.

Question No. III.

In an attempt to avoid misinterpretation the same idea has been phrased in another manner. Please check your reaction to the following statement: Generic differences could be compounded from specific differences.

( ) Yes. ( ) No. ( ) Question meaningless. ( ) Question obscure.
( ) No opinion on the subject.

To those who care for it a tabulated summary of the replies will be mailed. If you would like such a summary please make a check in the following space ( ).

The response to the questionnaire was most gratifying (Table 2). Practically all in the group checked their responses and a considerable number amplified the questionnaire with a discussion of the points which had been raised. It was immediately apparent that there was a very considerable relation between interest in the questionnaire and the age of the person replying. Among the younger men such expressions as "I am looking forward to this symposium" or "I have discussed your questions at length with such and such a colleague and they have stimulated an interesting discussion" were common. Many of the older botanists, on the other hand, answered with reluctance or expressed doubt as to the wisdom of the enterprise. By grading interest in four objective classes it is even possible to demonstrate this correlation in tabular form (Table 1). It is one

TABLE 1

Correlation between interest in the questionnaire and the age of those replying.

	UNDER 40	40 TO 55	OVER 55
Not in sympathy with questionnaire	..	..	2
Replied without comment	2	7	7
Replied with additional comment	6	6	5
Replied and also expressed interest in questionnaire	12	1	1

thing to demonstrate a correlation and another thing to interpret it correctly. In this case several factors are probably responsible for the correlation. Certain of the younger men might have been deferential towards the project, since I was older and presumably wiser. And for the same reason those older than I might have had less tolerance for a novel project by a much younger man. It is also undoubtedly true that the genus problem is so complex, and requires such a long apprenticeship, that few young biologists have enough experience to discuss it intelligently. The older men were experienced enough to realize this fact and to realize the complexity of the problem. One of this group wrote me as follows, and I quote his remarks because I find myself very much in sympathy with this point of view: "Your circular letter of August 26th does not arouse any warmth within me. All the questions you raise are purely speculative, and in the present state of our knowledge they cannot be answered. These problems work themselves out practically for each publishing taxonomist, and a

fair agreement has been reached as to the limits of genera and the limits of species without much reference to philosophical considerations. Discussion of such problems is likely to be made by persons who have no taxonomic training and the conclusions would be of little practical value. Probably I should not take the time to read them. Persons who have no actual contact in the diagnosis of species are likely to want definitions of what a species is. The taxonomist does not raise the question in that way, but meets each case as it come to him. Perhaps in a century or so from now we shall be able to approach such problems with sufficient knowledge to make the conclusions significant."

TABLE 2

Summary of 48 replies to questionnaire.

QUESTION I

Genus the more natural unit	26
Species the more natural unit	8
Sometimes one, sometimes the other	11
No opinion	1
Question meaningless	2

QUESTION II

Genera originate in the same way as species	31
Genera may originate in a different way	4
Genera may originate in same or in a different way	9
No opinion	4

In my opinion there is another, and more important reason for the correlation between age and interest. Many of our younger taxonomists have a different biological training from the older generations. Consequently they have a different attitude towards taxonomic work and that difference is reflected in the correlation shown in Table 1.

A large proportion of the replies warned me that I would find great differences of opinion on these questions. In the face of such statements it is particularly interesting that of the fifty replies received twenty-one were absolutely identical. A considerable proportion of the remainder differed only in one detail or another. Apparently therefore there is more agreement among modern taxonomists than they themselves realize. This orthodox point of view revealed by the questionnaire is that genera are on the average more natural units than species, that they originate in the same way as species and that generic differences could be compounded from specific differences.

The replies were then studied to see if there was any obvious correlation between the above point of view and the experience of the botanists who held it. Since there seemed to be a connection between monographic experience and "orthodoxy" an attempt was made to group the replies with

reference to the monographic experience of those replying. For this purpose it would have been ideal to have had twenty-five replies from botanists who had done nothing but monographic work and twenty-five from those who had done no monographic work whatever. Unfortunately there was no such clear cleavage and we had to content ourselves with selecting the following two groups, which have been called "monographers" and "non-monographers" to simplify Table 3 and its discussion. It would be more truthful to refer to the first group as "taxonomists whose experience has been rather exclusively in monographic work" and to the second as "taxonomists who are not monographers or who have had extensive experience in other biological disciplines."

Group I. "Monographers."

Blake, Epling, Fosberg, Gleason, Goodman, Greenman, Hitchcock, Hopkins, Johnston, Kearney, Munz, Ownbey, Pennell, Rosendahl, Sherff, Wright Smith, Lyman Smith, Svenson, L. O. Williams, Woodson, Yuncker.

Group II. "Non-monographers."

Anderson, Babcock, Camp, Cory, Deam, Hermann, Howell, Kinsey, Mattfeld, Merrill, Muenscher, Müntzing, Nelson, Palmer, Raup, Stebbins, Steere, Steyermark, Stockwell, Weatherby, Wiegand.

The replies of these two groups are tabulated in Table 3. It will be seen that even though the distinction between the two groups is somewhat imperfect there is a decided correlation. Two-thirds of the monographers are "orthodox" but less than one-third of the non-monographers.

TABLE 3

Correlation between monographic experience and "orthodox" opinion in regard to genera. Further explanation in the text.

	UNORTHODOX	ORTHODOX
Monographers	14	7
Non-monographers	6	15

SUMMARY

It should again be emphasized that the results of this investigation have probably little or no bearing on the question of genera as they may or may not exist as evolutionary units. The aim of the investigation was to ascertain something about genera as they exist in the minds of taxonomists. For a representative group of 50 taxonomists the following facts were established.

(1) There is a perceptible correlation between age and interest in discussing such concepts as genera. In part, at least, this probably reflects a

changing attitude towards taxonomic work. (2) Nearly one-half of those interviewed gave identical replies to the whole set of questions. (3) There is a very strong correlation between monographic experience and the tendency to the point of view that genera are more natural groups than species, that they originate in the same way, achieving their greater discontinuity by the disappearance of more intermediates.

<div align="center">CONCLUSIONS</div>

The results reported above and the various comments, which accompanied the replies, lead me to conclude that much taxonomic work is strongly colored by a widely accepted hypothesis. The notion that individual differences are gradually built up into varietal, and these progressively into differences of specific and generic rank is so logical that it has, consciously or unconsciously, been accepted by many taxonomists as absolute dogma. More than one systematist in replying to the questionnaire expressed astonishment that one might even consider evolutionary forces which would lead to the separation of genera but which would not operate in the formation of species. Yet by experimental analysis we already know of various quite different isolating mechanisms of evolutionary importance (Dobzhansky, 1937). It is scarcely credible that there are not others still to be discovered. We already know of mechanisms which may operate in the deployment of subgenera but may not in the deployment of species. It is already possible to indicate species which are separated by evolutionary forces different from those forming varieties within the same species (Anderson, 1936). The patterns of evolution are too complicated and too various for the universal application of any simple phylogenetic hypothesis.

For such reasons as these I find myself in sympathy with those who dissented from the "orthodox" view reported above. In my opinion it would be well if monographers could approach their work with minds unprejudiced by evolutionary theories. We are so certain of the fact of evolution that we are prone to forget how little we know about the forces behind it. Personally I find myself in complete agreement with the following comment which was appended to one of the replies.

"It looks to me as if you were trying to generalize on the assumption that there is a basic uniformity in taxonomic groups. There is nothing of the sort. Taxonomy is only a glorified guess—an attempt to construct a cross-section of lines of descent in a form intelligible to the human mind. It always contains two variable quantities—the plasticity of animate nature and the differing points of view of the people who work at it. You can generalize successfully, if at all, only by keeping these facts constantly in mind. I suspect that the situation is best expressed by the old aphorism:

the only general rule is that there is no general rule. Therein lies the fascination of taxonomy for those who like it. It is not a matter of mechanically applying a universal set of categories to given groups of facts. Each group one tackles presents a fresh and original problem; for each, one has to work out anew the method by which he may best achieve that transforming of confusion into order which is the great satisfaction of pure taxonomy."

NOTE:—When replies to the questionnaire arrived, I realized that there had come into my keeping, material which was of extraordinary biological interest and which would be of increasing importance in the future. I am accordingly having the replies bound, together with their accompanying letters, and deposited in the library of the Missouri Botanical Garden.

THE MISSOURI BOTANICAL GARDEN AND WASHINGTON UNIVERSITY
ST. LOUIS, MISSOURI

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III. Genera from the Standpoint of Morphology

J. M. Greenman

My concept of the genus has been formed through a practical expe-
rience in the field of taxonomy extending over a relatively long period of
years. It has developed gradually, but it was first formulated when influ-
ences brought to bear were on the whole conservative. I learned from my
teachers of biology, from my associates, and from my own observations,
that a genus is a taxonomic category consisting of one or more related
species, and that a group of allied genera constitute a family.

In simple terms then, but in degrees of diminishing importance, there
is the family, the genus, the species, and the variety. Other categories
may be interpolated if thereby clarity and convenience be enhanced.

Thus, classification is fundamentally a practical arrangement for
convenience—a means to an end. In other words it furnishes a ready instru-
ment for identifying any given plant and placing it in its proper pigeon-
hole. Little thought was given to any underlying principle or philosophy
concerning the classification. And I fancy that some botanists of today
look upon classification, or taxonomy, as being only such a mechanical
device. The basis of our present system of classification is quite another
thing, and it is of fundamental importance. It is the result of the experience
of many generations; and it rests primarily on comparative morphology.
Moreover, there is a definite philosophical principle underlying the sys-
tem, namely, the arrangement of the larger categories in such a manner
as to indicate, through comparative morphology, their genetic relation-
ships and to some extent their probable phylogeny.

No one now claims, no one has ever claimed, that the present system
of classification, namely, the one elaborated by Engler and Prantl, is per-
fect and final; but, that on the whole it expresses better than any other
system of classification previously or since. proposed a relatively natural
grouping of plants in accordance with our present knowledge of them.

Of the taxonomic categories mentioned above, namely, family, genus,
species, and variety, each category may vary to a considerable extent in
accordance with individual interpretation. That is the personal element
which has always been a factor and probably always will be so long as
the subject remains a dynamic one; but, even so there is almost always
a universal understanding as to what is meant by a generic category.

However, it is important to bear in mind that the concept of the genus,
as well as the species, may vary not only with the individual's interpreta-
tion, but it may vary more or less in accordance with the trend of the

times. This is perfectly natural, since we are all influenced to a greater or lesser degree by the opinions of our contemporaries.

At the present time taxonomists are working almost universally in accordance with the type-concept idea. That is, the species of a genus must conform in all essential morphological characters to those of the type-species of the genus under consideration, and similarly all members of a species must conform in the essential morphological characters to the type-specimen of the particular species concerned.

In the absence of a type-specimen, that is where there is no historical type extant, a standard-species may be substituted. Likewise in the absence of a historical type specimen of a given species a selected specimen may be taken as typifying the species. In accordance with this plan of operation, the generic concept centers around a concrete thing—the type-specimen. Whereas, formerly the generic and the specific concept centered around the complex which represents the genus or species in its general area of distribution, and more particularly the dominant form.

To show this change in concept, may I refer to an incident in my own experience (if you will pardon a personal reference). Some years ago, when I was a graduate student working under the direction of Professor Adolf Engler in Berlin, I recall very well one of the many discussions which took place during the lunch hour. The late Professor Ernest Gilg said to me, "Aber, Herr Greenman, was meinen Sie ueber das Wort Type oder Typus? Meinen Sie viellicht das Original?"

At that time in many of the great botanical centers in Europe and elsewhere the type-concept centered around the most common representative of the genus, as well as the species, in its total area of distribution rather than on the historical type. Again may I say that it becomes necessary to bear in mind the time factor involved when we try to interpret the delimitations of a genus or of a species?

Many genera, as now delimited in literature, have been greatly altered from the original interpretation placed upon them. Some of the older and larger genera now include many generic synonyms. Take for example *Andropogon, Panicum, Crepis,* etc. It not infrequently happens that generic names, which have been reduced to synonymy, upon a more intensive restudy have to be revived and given coordinate generic rank. This was shown to be the case with *Astranthium,* a genus proposed by Nuttall and reduced to synonymy under *Bellis,* but upon restudy by Esther Larsen (1933) it was revived and reinstated as a valid generic entity.

Another instance is that of *Youngia* of Cassini, a genus which was regarded for many years as synonymous with *Crepis,* but upon an intensive restudy by Babcock and Stebbins (1937) it has been reinstated by them as a valid genus.

I mention these examples, because it is impossible to treat all genera in exactly the same way; not infrequently are they differently constituted, and must be treated accordingly.

Apropos of the lack of uniformity in genera, may I say that new genera have been proposed in the course of studies made on the flora of a limited region; and while it is true that such genera appear to be amply distinct when compared with other genera of the same region, yet when studied in relation to the entire representation of the genera concerned, the newly proposed entity is not infrequently found to be merely a variation. Hence, it is very important in formulating our concept of a genus, and of a species also, to take into consideration not only comparative morphology, but also geographical relationships. This principle, I think, has been well demonstrated by Dr. H. K. Svenson in his work on *Eleocharis*.

Much has been said about the segregation of genera. I am not opposed to segregation if it can be justified on the basis of comparative morphology, including characters not previously recorded, and the application of any supporting evidence obtained from anatomical studies, cyto-genetic investigations, or any other sources of information. We should recognize the desirability, however, of keeping the generic category as uniform as possible.

Unless some very definite object is attained by segregation of relatively homogeneous groups of plants, such for example as *Aster, Erigeron, Conyza, Baccharis, Senecio, Euphorbia,* and *Cassia*, I am personally inclined to think that it is more practical to retain these groups in their traditional sense. Certainly such a treatment is less disconcerting to botany in general than to make numerous possible changes. Generic segregation almost invariably means the introduction of new combinations and new names.

After all *Aster, Erigeron, Conyza,* and *Baccharis* are not entirely and mutually exclusive categories, any more than are *Cirsium* and *Carduus;* since, when one studies large series of specimens representing these genera, it is manifest that they grade imperceptibly one into another. But largely for the sake of convenience they are maintained as separate genera.

If one began to segregate the genus *Senecio,* as it is usually interpreted, it would be possible to recognize some twenty or more genera in which habit would play a prominent part. Difference in habit is due primarily to change of environmental conditions. And when one studies this genus throughout its entire geographical range, which is not exceeded by any other genus of flowering plants, it would be exceedingly difficult to maintain the possible generic segregates. Furthermore, the number of new names and new combinations would be excessive and confusing.

On the whole, therefore, my personal inclination is towards a conservative concept of the genus and the retention of well-established generic names in so far as consistent with the comparative morphological characters originally ascribed to them, especially when corroborated by additional knowledge gained by a more intensive study resulting from improved technique and new methods of attack.

Finally, may I say that while I am of the opinion that comparative morphology must remain as the fundamental basis of classification, yet I welcome the important contributions to taxonomy, which have been made through cyto-genetic studies and experimental investigations.

THE MISSOURI BOTANICAL GARDEN
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IV. The Delimitations of Genera from the Conservative Point of View

Earl Edward Sherff

It may seem presumptuous to attempt to represent within twenty minutes, even in small part, the conservative school of thought in plant taxonomy. In fact the term conservative itself has been sadly abused and one doubts if its definition for botanists generally is not largely subjective and dependent mainly upon who does the defining. By one writer conservatives have been characterized as those seeking relationships and hesitant to describe new species, while radicals are characterized as being impressed by diversification and anxious to record their findings. But with many of us the distinction seems akin to that made long ago between orthodoxy and heterodoxy, namely, that orthodoxy is my "doxy" and heterodoxy is yours. Certain it is that some taxonomists have professed a conservative viewpoint for generic delimitations and then, by utter disregard of nomenclatural rules or taxonomic precedent, or both, proceeded to make wholesale changes or innovations of nomenclature in other respects, sometimes going farther than even a self-respecting radical or liberal would feel warranted in doing. Thus, for example, what amounted almost to an obsession with one of our late American workers in taxonomy was the designation and naming or renaming of subspecies, by which he meant commonly nothing more or less than the conventional varieties as they were understood by Linnaeus, Augustin DeCandolle, Willdenow, Gray, and a long line of other workers. If we are to accept the principle of a binomial nomenclature at all, it would seem self-evident that we should not only abide by the rules adopted by our international congresses but also, wherever an arbitrary choice is to be made, defer to the carefully reasoned practices and matured judgments of taxonomy's founders, whenever these practices and judgments do not conflict with present-day rules.

Both radicals and conservatives must use the binomial system of nomenclature. An essential feature of this system is, of course, that the binomial for any species derives its first part from the generic name. This feature has been lamented as a fundamental weakness of the binomial system, since a change in our conceptions of genera and species eventuates frequently in a change of the scientific names. L. H. Bailey even states that "we should have gained much in simplicity of literature, in clarity and in popular usage, if we had had a mononymy or other arrangement instead of a taxonomic dionymy." Even admitting the truth of this statement, should we not have lost immeasurably had nomenclature failed to asso-

ciate for us, as it attempts to do under the binomial system, related specific entities under one generic name? In any event, as long as the binomial system of nomenclature is officially used by all of us, truly conservative botanists will be reluctant to recast generic concepts or limits except upon the most convincing evidence.

Conservatives, generally, speaking, attempt to delimit genera with approximately the scope employed by Tournefort and later by Linnaeus. To sneer at our inability to define categorically what is meant by the Linnaean concept of genera is beside the point. True, there has been inconsistency, but it likewise is true that an unbiased study of Linnaean genera usually imparts a *genus sense* which is not far off the middle road of taxonomic opinion. Apparently much of the mischief done heretofore in carelessly juggling generic limits must be blamed upon certain view-points and procedures which the conservatives must condemn if they are not to condone the mischief itself. May we mention a few of these very briefly.

First there is the loose talk heard in some quarters about cumbersome trinomials and quadrinomials. In case a cosmopolitan or at least polydemic species exhibits several varieties and forms or *formae*, we are in effect told to elevate each to specific rank and thus simplify our nomenclature. A logical outcome of such a course, however, is sure to be the warping of our *specific* concepts far past the limits understood for species by Ray or by Linnaeus. In short, we shall have a degradation of the original species concept in numerous cases but its retention undisturbed in the others. Some of our so-called radicals, having committed themselves to this way of doing, have awakened to find too many species in some of the genera. They have then made generic segregations to ease the fancied tension from within which they themselves had helped to create. If we are truly enamoured of conservatism and genuinely believe in a logical delimitation of genera, we must not neglect our *species* concepts.

Another matter that must engage our attention is the provincialism that has flavored all too much of the work on the manufacture of new genera. The entire earth must be taken as the source-book of our generic concepts. The writers of some of our manuals and local floras have over-looked this fact. Many times they have erected so-called new genera largely or solely upon the basis of the species within their own geographic range. A classic instance is that of *Astragalus*, where the author of a manual covering part of western North America decided to employ eighteen distinct genera instead of one. But, as Skottsberg, a distinguished representative of conservative opinion abroad, points out, *Astragalus* is not exclusively or even mainly a North American genus. "Is it likely," he asks, "that the eighteen United States genera will be left untouched and natural after

the 1,000 non-American species have been taken into due consideration?"
Skottsberg sets forth additional examples, one of them that of *Vaccinium*
as treated in American manuals. For the American species, the keys to
the sections *Vaccinium* proper, *Cyanococcus*, and *Vitis-Idaea* are suffi-
ciently diagnostic. When, however, a half-dozen mutually close Hawaiian
Island species are compared with the same keys, they are found to run
to different sections, or indeed to possess overlapping characters. A
believer in small genera might here be inclined to put *Cyanococcus* and
Vitis-Idaea as separate genera and erect one or two additional but tiny
genera to take care of the Hawaiian misfits. A conservative course would
doubtless be, on the other hand, the continued maintenance of the genus
Vaccinium in its broader sense, coupled with a redefinition of the com-
ponent sections. A point to be emphasized, however, is that the author of
a local flora or a manual for a restricted range is many times unfamiliar
with a considerable percentage of species in the genera treated. In most
cases the presumption of evidence will be against him. The least he can do
and at the same time show respect for other workers who must use his
book is to refrain from altering the status of any genus unless he has a
comprehensive monographic knowledge of it for whatever parts of the
earth it may inhabit.

A third matter, one closely related to the second, is the need for greater
emphasis upon monographic research. It may be true, as some able workers
assert, that various large genera like *Opuntia* and *Euphorbia* need break-
ing down into smaller units if we are to have a genus concept such as Lin-
naeus would have formulated could he have had all the information that
we possess today. But only extended and painstaking monographic research
will be of much value in helping us to make the appraisals or evaluations
needed for settling these cases. May I inject here my own personal con-
viction, intensified during several years' monographic research upon the
genus *Euphorbia* as it occurs in the Hawaiian Islands? I recognize of
course that a large genus may embrace species more diverse morphologi-
cally than species of many admittedly distinct Linnaean genera. Such a
genus is apt, however, to display within itself such a profusion of inter-
grading and overlapping characters as to make clean-cut generic segrega-
tions, at least within our present geological era or epoch, quite impossible.
Conservatives are stigmatized as inconsistent if they move slowly in accept-
ing some of the proposed segregations. But of what use is it, we may well
ask, to reach for imagined increase in consistency if in so doing we throw
the species into such confusion that no honest student can successfully
fit to them our binomial system of nomenclature.

The conservative's preference in a general way for stability in nomen-
clature is sometimes criticized as making for stagnation of taxonomic

progress. One botanist has rightly termed the hope for complete stability a "will-o'-the-wisp calling us to the swamp of unattainment." But surely no conservative hopes for or expects complete stability. New forms continue to be discovered and, with their study, limits of certain genera may have to be changed. Old genera that have received their present taxonomic identity largely by piecemeal accretions from the pens of numerous authors must needs be restudied monographically. Much has been written about polyphylesis, or the origin of a genus or other group at different places or times by convergence of two or more lines of descent. Little has been written about the *pseudo-polyphylesis* that has arisen sometimes in literature when two or more authors with diverse points of view have referred generically different forms to the same genus. Conservatives, however, should be and doubtless will be as prompt as any others to welcome a re-examination of the morphological and phylogenetic bases on which each such genus rests. They will insist none the less that major nomenclatural changes be made only after extended and detailed research and not as the result of personal whim, or caprice of fancy, or mere love for something new. Probably our present era exceeds all past eras in the tendency to mistake mere change for genuine advancement. The plain duty of taxonomists, whether of the conservative or radical persuasion it matters little, is to shun all change made merely for the sake of change. They must seek an atmosphere of the utmost objectivity for their researches. It would be false to say that our concepts, generic or otherwise, are never in part subjective, but the degree of subjectivity should decrease as the comprehensiveness and thoroughness of our work increase.

A word should next be said against the arbitrary separation of genera, as is still often done, solely upon the presence or absence of one or more supposedly diagnostic characters. Under the theory of special creation this may have seemed justified. But we cannot hope to reconcile our presently held evolutionary theory of phylogeny at all points in the plant kingdom with such a practice. The genus *Cosmos* may be taken as an illustration. If we insist upon the presence of a rostrate achene, as was once done, several undisputed species of *Cosmos* automatically fall out of the genus, among them *Cosmos calvus*. If we insist upon wingless achenes, then *Cosmos Blakei* is excluded. If we demand slender roots, the entire section *Discopoda*, characterized in part by having fascicled, tuberous roots, must be dropped. Yet *Cosmos*, whether we assume for it a monophyletic or a polyphyletic origin, is so natural a genus that it was not even divided taxonomically into sections until 1932. The presence or absence of retrorsely barbed achenial aristae in the separation of the genus *Bidens* from the genus *Coreopsis* offers another illustration. Linnaeus, Augustin

De Candolle, and a host of other workers separated the two genera primarily by this one character. When Asa Gray found a herbarium specimen of the so-called *Coreopsis aristosa* possessing retrorsely barbed aristae instead of the antrorsely barbed ones customary in that species, he designated it "*Coreopsis aristosa* transformed into a *Bidens*." Later he treated this and similar forms in his *Synoptical Flora of North America* as hybrids between *Coreopsis* and *Bidens*. But with the advance of knowledge that came during the decade following the appearance of Gray's *Synoptical Flora*, it became evident that these forms were not hybrids. On the contrary, they were recognized as definite varieties. We then had the anomalous situation in which *Coreopsis aristosa, Coreopsis involucrata*, and *Coreopsis trichosperma*—to use the names then accepted for these species—were assigned to *Coreopsis*, while their varieties with retrorsely barbed aristae were to be referred to another genus, *Bidens*, if the traditional basis of distinction were to be observed. N. L. Britton promptly sensed the utter inconsistency and indefensibility of insisting further upon the following of tradition—and here we digress to remark that Britton would rank with most of us as a liberal or radical, not a conservative. Yet the course that he adopted in this and many other instances, when contrasted with that previously followed by some who were professedly conservative, should remind us that not all taxonomic progress has been accomplished or even initiated by the conservatives. With this thought in mind, may I confess to almost an outright fear of doing violence to the interests of plant taxonomy by appearing to divide its devotees for even twenty minutes into two distinct schools of thought? In actual experience there are more than two schools and each school has several grades. Moreover, the enrollment is frequently shifting and sometimes even switching schools. But to return to the case in point. Britton at once referred the so-called *Coreopsis* species exhibiting ambiversalism in their aristal barbs to the genus *Bidens*. In so doing, he was guided not by a single arbitrary or artificial character but by the sum total of characters manifested in each group studied. Such a course, it would seem, conservatives must ever stand ready to adopt if our taxonomy is to take even the slightest cognizance of evolutionary phylogeny.

This brings us to the often heard criticism that considerations of phylogeny will forever upset nomenclature. In the multitudinous cases like those mentioned, however, it will usually be only one or a few of the borderline species that will require shifting and consequently a change in name. The genera themselves will stand largely intact. But even in cases where the supposed phylogenetic record would appear to dictate radical rebuilding of generic concepts or widespread shifting of generic limits, it should be remembered that phylogenetic preachments vary highly

with the one uttering them. They may reflect a complex of emotional, nutritional, economic, and, someone has been cruel enough to add, pathological factors, a complex that has been known more than once to express itself in distinctly different phylogenetic explanations by the same individual within successive periods of time. Here, may I say, all true conservatives should welcome carefully thought out contributions from the standpoint of phylogeny, but we can have little patience with ever-recurrent, petty tampering in generic limits. Especially must this be so if we are led to suspect that a fortnight's sojourn at the seashore or a different brand of breakfast food would have crystallized into a different phylogenetic scheme of relationships. A recent writer has pleaded for a freer use of subgeneric sections to avoid the needless multiplication of genera and consequent alteration of numerous binomials. And indeed it would seem that there is much to commend such a plea, especially for the many cases where equally competent and equally well-informed authorities disagree.

Passing over several additional considerations which are germane to the subject of generic delimitations but which must be omitted here for lack of time, I shall conclude by discussing for a moment the urge made upon us, that we turn to experimental taxonomy, especially in its ecological and genetical aspects. As was pointed out by De Wildeman some years ago and also by Wiegand, the data offered by experimental taxonomy are not usually of practical value to the general taxonomist, even though they are very desirable and often capable of throwing great light upon the significance of morphological characters. To quote Wiegand verbatim, "such data are often impossible to obtain, sometimes because of the unavailability of the living material, sometimes because, as in the case of woody species, the time required to grow the plants is too great, but often also because of the large number of plants concerned." Personally, I would be the last to discourage monographers anywhere from supplementary cultural studies. But if it be admitted that generic characters as a rule are especially well ingrained into the evolutionary fiber of plant species, it would seem that limits of genera, as apart from limits of smaller units, will not soon need alteration because of experimentally adduced evidence. It appears not unlikely that far into the future, as already in the past, we must perforce heed the counsels of morphology and ofttimes of geographic distribution in the delimitation of genera for all unless some of the very lowest plants.

CHICAGO TEACHERS COLLEGE AND FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, ILLINOIS

V. Our Changing Generic Concepts

W. H. CAMP

So far during this symposium there has been presented a most interesting discussion concerning the concept of the genus. Professor Bartlett, in his inimitable manner, has traced the early history of the concept of this unit of nomenclatural biology. Dr. Anderson, by means of his questionnaire, has collated and evaluated the thoughts and ideas of various of our modern taxonomic workers on the status of the genus. To this much-discussed problem, and based on patient study and much thought, Dr. Greenman has added his personal concepts. And Professor Sherff, using stability as the pillar around which he built his most excellent discussion, has presented a few of the many and valid arguments for the perpetuation of this stability.

It is therefore fitting to remember that the thing which we as taxonomists have been praying for—and even legislating for—is nomenclatural stability. It is the bright star toward which we have been steering; the goal we have been striving for; the haven of dreams come true—where there shall be no more changing of names.

But before I proceed with this discussion it might be well to make a public confession. Surrounded every day by herbarium cases in which repose specimens labeled with more than 150,000 different names, I am opposed to any changes which will necessitate the learning of new ones for the pitifully few of those I do know. At heart, therefore, I am a taxonomic conservative, a worshipper at the altar of nomenclatural stability. But even so, I trust you will permit me my brief moment of intellectual agnosticism while I depart from the broad path of fundamentalism; while I chance the difficult way of the transgressor along the stony road of the one whose assigned task on this program is to discuss, with sympathy, a most unwelcome topic—the splitting of genera.

What the name of an organism might be would make no difference, if it were a name and nothing more; but, under the present system in taxonomy, there is an implied consanguinity, an expression of relationship between species in so far as the generic name is concerned. We find today, therefore, that the genus is less a taxonomic catch-all and increasingly a unit expressive of close phyletic relationship.

Thus, among professional taxonomists, two schools of nomenclatural thinking in regard to generic delimitation have arisen and are now pursuing their own ways. At times during the development of the science these concepts were intertwined, often they ran parallel and, today, some

workers in the one group feel that the concepts of the other are so divergent from a fundamental convenience that they plead for legislative fiat to control their activity. An activity which those who pride themselves on being called conservatives consider as chaos, but which by the others is thought of as scientific progress.

Now, for a moment, let us consider certain of the backgrounds of one of these schools of thought in regard to biological nomenclature. At all times in the present discussion, we must remember that most of the genera around which the present controversy centers were described, and therefore delimited, during that period when biologists held as a basic principle the doctrine of Special Creation and its necessary corollary, the immutability of life forms. The philosophy of those who hold to a traditionally rigid concept of specific and generic delimitation was therefore founded on the basic assumption of a Special Creation. They will deny it, but the evidence is so obvious that they are in error if they try to rationalize their concepts in any other way. We may only hope that they really believe differently.

However, even in the early days, the facts, those insidious things which are continually raising their sinister heads, began staring the fathers of our science in the face and they soon began to be troubled with the knowledge that a nomenclatural unit was a concept and not a fact; that there were no hard and fast lines between the separate entities of each taxonomic category; that not only species, but genera and even families might intergrade. But these things came late in the making of the science and long after the definitions of the classic genera were laid down. I cannot emphasize it too strongly: those who are most intent upon the retention of the nomenclatural *status quo* are, today, confronted with the task of trying to rationalize a static system of immutability with the known facts.

Perhaps the central idea back of this should be expanded, not that all of us do not understand the situation, but merely to put it in a more concrete form. Briefly, our present system of nomenclature, in a general way, is organized on a basis of similarities, having as its fundamental principle a doctrine based upon the thesis that a community of similar morphological structures indicates relationship. With this criterion established, the beginning student of taxonomy soon learns that the species of a single genus have more characters in common than do the sister genera which constitute a family. But as his studies progress, it is not long until he discovers that there is no equality in the standard of delimitation; that in one group of plants, those characters which scarcely constitute specific differences, in another may be sufficient to separate the genera.

For example: in an attempt to rationalize the Vacciniaceae (if I may be permitted to speak of them as a family and not part of the Ericaceae)

I am confronted with the situation of finding, in the classic treatments, that such things as the articulation of the pedicel, which serve in part to separate the genera of the Thibaudieae, are in the Euvaccineae not considered as having sufficient weight to be included as characters separating even the species.

Let us now, for a while, consider another phase of this problem: certain of the goals of taxonomic research. As I have intimated, there are, at the present time, two rather definite schools of taxonomic revisionists. One of these includes those who, in their revisions, follow the already established generic lines, their work consisting in part of weeding out the synonymy that has, perhaps unavoidably, slipped into the literature of the group and also listing or describing the new material found since its last monographic treatment. The other school is not so much interested in the mere cataloging of known species as in a study of the origin, evolution and dispersal of a group of plants. It is this group to which the epithet of "splitter" is most often applied. It can only be regretted that some of the worst offenders in this matter were not so much monographers, but students of regional floras and, although much of their work undoubtedly will be permanent, it serves temporarily, at least, only to becloud the main issues. On the other hand, the honest monographer studying the group on which he is engaged from the standpoint of its total distribution, sees it as a group of plants which are the result of divergent lines that have proceeded out of the world's dim past into the present and knows that the plants in his hands, in themselves, do not constitute an orthogenetic series but are only the ends of a much-branched and often tangled system of descents. The monographer with such a viewpoint is likely to have a vastly different concept as to what constitutes a genus from the one who is merely cataloging the valid species of a group. I have not said that one method is better than the other, nor do I more than intimate that one is to be desired rather than the other. *They are intellectual activities of different sorts and, as a result, their end-products will be different.*

With this in mind and of myself knowing nothing about the mosses, I recently wrote to one of our well-known bryologists[1] for his opinion on what has been happening to the classic genera of bryophytes. I shall quote from his reply:

"There has been a tremendous change in the concept of the genus in mosses and hepatics in the last century. In the time of Linnaeus there were very few genera. Nearly all the acrocarpous mosses were members of *Bryum,* although the atypical and characteristic *Buxbaumia* and *Polytrichum* were, of course, recognized. Almost all pleurocarpous mosses were put into *Hypnum,* although, again, the absolutely unmistakable *Fontinalis* and *Neckera* were even then

[1] Dr. William Campbell Steere.

segregated. In the middle of the nineteenth century, however, a great splitting of the Linnaean and Hedwigian genera was effected in the epochal work of Bruch, Schimper and Gümbel (*Bryologia Europaea*) which was published between 1836 and 1855. The most important splits made here were the recognition in the old genus *Hypnum* of natural groups as new genera, such as *Brachythecium, Amblystegium, Plagiothecium, Thuidium, Pseudoleskea, Heterocladium,* and a dozen others.

"When the Musci of the whole world were evaluated as a group, rather than as an extension of the local flora of Europe and the United States, it was realized that mosses placed closely together in the same family, or even as congeners in the earlier systems, were really far separated. Through the work of Müller, and later Fleischer and Brotherus, whole new families and genera were erected for well known species. Whereas Linnaeus and, fifty years later, Hedwig, recognized a dozen or two genera, the list of valid genera in the last edition of Engler and Prantl (vol. 11: 1925) takes several pages. The tendency now is not so much to erect new genera, but toward a general recognition of splitting done since the turn of the century by Fleischer, Brotherus, Cardot, *et al.* However, I recall a paper by Dixon since 1930 in which he described ten new genera!

"It is therefore obvious that the breakdown in the Musci, insofar as the generic concept is concerned, is general. Now for examples. Perhaps the best are those from well known sources, and so I shall make a few comparisons between the old familiar Grout's *Mosses with Hand-lens and Microscope* (1903), and the newest and best, yet conservative work of Grout (as editor) *Moss Flora of North America, north of Mexico. Dicranum fulvellum* and *D. Starkei* are separated out into the genus *Arctoa. Dicranum longifolium* is now the type of *Paraleucobryum.* Although Grout does not segregate *Dicranum flagellare* and *D. montanum,* many American bryologists call them species of *Orthodicranum.* Still other segregates are recognized by Engler and Prantl. *Funaria* has been split, yielding the genus *Entosthodon.* The old genus *Amblystegium* has been broken up into *Amblystegium* (emend.), *Hygroamblystegium, Leptodictyum,* and *Sciaromium. Calliergon* yields *Calliergidium* and *Calliergoniella. Hylocomium* yields *Rhytidium, Rhytidiadelphus,* and *Rhytidiopsis.* Several other genera are split out by Fleischer, but not yet accepted by Grout. Even the much pared genus *Hypnum* still yields new genera, for example: *Brotherella, Heterophyllium, Ptilium,* and *Ctenidium. Plagiothecium* is subdivided into *Plagiothecium* (sensu stricto), *Taxiphyllum,* and *Isopterygium.* Grout considers these as subgenera, whereas Fleischer considers them as genera *in different families!* This very nicely illustrates the local viewpoint versus the cosmopolitan.

"I predict that I shall see all present subgenera become genera within my life-time. Splitting will continue almost anywhere in the mosses, perhaps most logically in the pleurocarpous groups. Hepaticae are in even more of a flux,

taxonomically. I am not unfavorably inclined or disposed toward these changes, for it is my conviction that most of the living forms are the tips of widely separated branches of the phylogenetic tree and are grouped together anyhow only because of man's passion for classification."

What I have just quoted from the above communication concerning the bryophytes is equally true of other forms. Let us, therefore, turn our attention to the flowering plants and for a little while consider the genus *Gaylussacia*, the huckleberries, with which many of us are familiar. The erection of the genera *Buxella*, *Decachaena*, and *Lasiococcus* to take care of our North American species of huckleberries has met with a great deal of opposition and I, too, have deplored the segregation.[2] But, fundamentally, it was sound, for the old classic genus is composed of four very definite groups of species: (1) The Buxifolicae (*Gaylussacia* H. B. K.), found mainly in the mountains of western South America, is composed of numerous species; (2) the Baccatae (*Decachaena* T. & G.), with its four species, is confined to eastern North America; (3) the Dumosae (*Lasiococcus* Small) ranges on the Coastal Plain from Newfoundland to Florida and Louisiana with two species, and occurs again with several additional in Brazil (a perfectly natural distribution); and (4) *Gaylussacia brachycera* (*Buxella* Small; this nomenclaturally a homonym) with an interesting distribution in small isolated areas from Tennessee to Pennsylvania and its morphological peculiarities, is plainly a relic out of the Early Tertiary and not closely related to the other huckleberries.

Had we been able to maintain the species with which we are most familiar in the genus *Gaylussacia* and erected new genera for those in South America, there would have been little protest. Apparently it is a common reaction among taxonomists—being human—that, so long as a genus is endemic in some remote part of the world it may be split as the student pleases, the splitting being hailed as a brilliant piece of research. But let one among us attempt, phyletically, to rearrange a genus with species in our own local areas—the rearrangement resulting in the necessity of learning new generic names—there is an immediate and loud protest. Even so, *Lasiococcus dumosus*, *Decachaena baccata* and *Buxella brachycera* are names with a strange and unfamiliar sound and I don't like them any more than you do. But, I have been asked, "Then why change them? We have known them as species of *Gaylussacia* for so many years." There is only one answer. If such an argument is to determine our criteria concerning the status of a generic name, then let us be purists and return these species to the genus *Vaccinium*, for they were known as *Vaccinium dumosum*, *Vaccinium resinosum*, and *Vaccinium brachycerum* for about a

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[2] Bull. Torrey Club 62: 129–132. 1935.

half-century prior to their inclusion in the genus *Gaylussacia*. The point is, none among us remember the clamor that arose when the botanists of another day had to learn to think of them as belonging to "that new-fangled genus *Gaylussacia*." From the standpoint of phylogeny, there is no more reasonableness in retaining these species in *Gaylussacia* than in returning them to *Vaccinium*.

Let us now turn our attention, briefly, to the Compositae. There immediately comes to mind the present controversy concerning the status of *Euthamia*. Is it to be a genus or merely a section of *Solidago?* If, however, we are truthful with ourselves, we must admit that the characters which we use to separate *Euthamia* from *Solidago* are of no less magnitude than those by which the basic species of *Solidago* and *Aster* are differentiated. Or conversely, if we return *Euthamia* to *Solidago* then, to be consistent, *Solidago* and *Aster* should be united. Or, for another example, the genus *Senecio*. Here is an open field for the taxonomist who wishes merely, either to describe a considerable number of new species or, as is not unknown to some of us, the pleasant experience of throwing a vast number of names into synonymy. Actually, however, the real opportunity for study in this genus lies in unraveling the various migration routes used, and the evolutionary mechanisms resorted to, by this cosmopolitan, highly divergent and exceedingly complex group of plants.

I am anticipating the question which the so-called conservatives will ask at this point. "Is it necessary that we have a whole host of new genera foisted upon us; will not the sub-genus satisfy your desire to express phyletic segregation?" The answer, flatly, is "No." Do these same "conservatives" advocate returning *Marchantia* to the Algae, all the species of lichens to *Lichen*, many of the mosses to *Bryum* and *Hypnum*, and a host of orchids to *Orchis?* So far, our science has been progressing steadily toward a rationalization between taxonomic categories and phyletic units, and I see no valid reason why we should make our nomenclatural system so rigid and unyielding that it would no longer serve to express what it traditionally has: *the rank and degree of relationship between organisms.*

This concern over "stability of names" has always been a point of discussion among botanists, and if taxonomic priority in the Spermatophytes goes back to the "Species Plantarum" so does the present controversy, for in 1753 Peter Collinson (probably the father of "modern" nomenclatural conservatism!) wrote to Linnaeus as follows:[3]

"I have had the pleasure of reading your 'Species Plantarum,' a very laborious and useful work, but my dear friend, we that admire you are much concerned that you should perplex the delightful science of botany with

[3] Clute, Willard N. The Common Names of Plants, p. 13. 1931.

changing names that have been quite well received and adding new names quite unknown to us. Thus, botany which was a pleasant study and attainable by most men, is now become by alterations and new names, the study of a man's lifetime, and none now but real professors can pretend to attain it. As I love you, I tell you our sentiments. . . . If you will forever be making new names and altering good and old ones for such hard names that contain no idea of the plant, it will be impossible to attain a perfect knowledge of botany."

Being thus fortified with the knowledge that today's controversies are not a new thing and buoyed by the hope that the science of taxonomy has not become stagnant, I trust that we may look upon our present minor tempests with the same patient humor with which we view those of the past. Thus, looking into the not-too-distant future, we may envision the day when our standard texts will list not more than a half dozen species of *Vaccinium* in the Americas for, after all, the high-bush blueberries of our eastern states are much more closely related to the secure and well-established *Thibaudia* of South America than to *Vaccinium Myrtillus*, the type of its genus, the one which Linnaeus described first because he knew it best.

Perhaps I speak with unreasoning rashness, but in a science where every thinking morphologist and vascular anatomist knows that the "Pteri-dophyta" are not a phylum; that the "family" Polypodiaceae is not mono-phyletic but, in the main, a miscellany of the end-products of the evolu-tion of other basic fern families; and where nearly every taxonomist admits that the Compositae are polyphyletic and not a natural family—and yet does nothing about these things—it is small wonder that the honest phyletic revisionist, too often confused with the unreasoning splitter of genera, is looked upon as a botanical outcast and pariah.

I tell you, and I am serious, we as taxonomists must face the issue. Either we must take our place with those who are attacking the funda-mental problems of biology, or we will degenerate into mere namers of speci-mens. We must either confine ourselves to the grinding out of a few lines of miserably inadequate Latin with *sp. nov.* and our names hooked onto it, or be biologists. The bifurcation is clear. And if we are to take our place in the body biologic, it can only be as phylogenists—students of evolution in the broad sense—with the naming of plants a mere incidental. In doing so, we will find it necessary from time to time to reconsider our premises for, with additional information, it will be necessary to reorganize our concepts and lay our course into new channels of thought.

At present, our nomenclatural system indicates phyletic relationship. If we continue this system—and I see no need to change it—the results of our work must then be reflected in the names we use. Actually, owing to

fortuitous segregation of the past, *the number of changes necessary would be much less than one might suppose.*

If I am correctly informed, the first organized part of botany was taxonomy. Morphology and comparative anatomy have long ago forgotten the manner in which they were born, and cytology has bred a line who look upon their sire with pity and a little contempt. It is perhaps advisable that they again be brought in as integral parts of the family circle. Yet, in honesty and fairness, their defection was no fault of their own. It was ours. When they were born we tolerated their blattings as we do those of infants. In adolescence we were blind to their needs and gave them little guidance and less help, refusing to see that as adults they might have something of their own and something to contribute to our needs. It is therefore little wonder that morphology, comparative anatomy and cytology, pursuing their own ways with but little concern and less guidance from their parent, should be little troubled with the trials and tribulations which now confront their sire.

Casting aside simile, I say: it is high time that we as taxonomists make better use of the findings, and particularly bring into play the techniques of the modern morphologist, the comparative anatomist and the cytologist. Frankly, those of us who blat loudest "Back to the fundamental truth—back to Linnaeus," are those who have made little or no use of the wealth of material already made available to us by the students in these other fields.

The space is limited and I cannot, here, present my case with specific examples where such studies have been made and the conclusions derived from them but, in general, if we were to apply the techniques available and reconsider the problems confronting us from the standpoint of phylesis, some of our existing genera would be combined and still others be broken down into their proper units. This, obviously, necessitates the change of some few names. But what of it? Should we, in deference to the non-taxonomists—a vociferous group who think of their branches of the science as being progressive—hesitate to modernize our science, even at the expense of a few changes of name? Do we as biologists hold that Aristotle taught only truth? In spite of their fad for "standardized plant names," do the horticulturists still use the nomenclature of Pliny? Do the physiologists feel the necessity of discussing their phenomena in the phraseology of Stephen Hales or Lavoisier? Do the ecologists use only the concepts of Warming? Do the anatomists describe their structures in the terminology of Marcello Malpigi or Nehemiah Grew? Do the cytologists consider Robert Brown the sole authority on nuclear phenomena? Are we, the taxonomists, then, to be stuck forever with concepts of the limits of genera as defined by Linnaeus, by Bentham, or even Asa Gray? If we are

honest with ourselves, we will admit that we have not felt any such necessity in the past. Nor do I see any present need of maintaining a stultitiously archaic *status quo* if, in holding to it, we impede the splendid progress already begun in a better understanding of fundamental plant relationships.

Perhaps we should adopt as our motto, not "Back to Linnaeus" but, "Forward to the truth." Perhaps, if we were not afraid of the puling croaking of certain of our confreres every time we broaden and particularize our concepts, we could put new life into old taxonomic bones, long interred in the musty vault of nomenclatural conservatism.

From an increasing number of laboratories there come rumblings of a rejuvenant taxonomy and I warn you, the workers in these institutions are not merely worms working in the corpse. When their further results come, as they recently have, there are those among us who may not like them, for a few plant families will be ripped apart and genera will be recast. Perhaps, with a regenerate and growing science—contributing more to botany than several additional lines to the latest supplement of the Index Kewensis when we revise a group; when we become a real part of biology —with emphasis on the true meaning of $\beta\iota os$—we then can move out of the top floors, the dusty attics and dim holes where they have pushed us and down where we belong—down on the first floor with the rest of those who, too, consider themselves botanists.

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The Cytology of Sporangium Development in Azolla filiculoides

ROBERT E. DUNCAN

(WITH 30 FIGURES)

INTRODUCTION

The genus *Azolla* has long been of interest to investigators as one in which heterospory and a most striking case of tapetal behavior can be studied. In a classic monograph Strasburger (1873) presented the results of his morphological and histological researches on *Azolla*. He found that a leaf originates from the upper two ranks of epidermal cells of the stem. The first division of such a cell, in an anticlinal plane, forms an upper larger and a smaller lower cell. From these cells the two lobes of a mature vegetative leaf develop. In the development of a sporophyll the lower cell gives rise to a sporocarp and its hood-like covering instead of to the small lower lobe of a vegetative leaf.

Campbell (1893) considered that the hood represents a modified upper leaf lobe. Goebel (1898) held it to be merely an outgrowth from the under side of the upper leaf lobe. The sporocarp initial is foliar in origin (replacing the lower leaf lobe), grows for a time as does a leaf initial, then dichotomizes so that the ensuing sporocarps appear in pairs. Sud (1934) doubts the foliar origin of sporocarps in *A. pinnata*.

Strasburger (1873) reported that a sporocarp develops by means of an apical cell with three cutting faces, whose activity results in the formation of a columella or basal region from which sporangia later arise. About the base of the sporocarp initial appears a collar-like growth which, as the columella elongates, develops into the indusium or sporocarp wall, two cells in thickness. The primordia of macro- and microsporocarps are similar; a short-stalked macrosporangium is present in every case, but in a microsporocarp it ceases development early—being represented by the club-shaped end of the columella first described by Meyen (1836)—and microsporangia develop from initials at the base of the columella. In the developing macrosporocarp Campbell (1893) found that the apical cell of the columella forms a terminal macrosporangium. Goebel (1898) held the columella to represent an abortive macrosporangium.

In contrast to these points of view, Griffith (1844) observed that a terminal sporangium is present in every sporocarp but that in certain cases this sporangium collapses and other sporangia develop from below its base. Pfeiffer (1907) confirmed this observation, finding that the dif-

ferentiation of sporocarps is entirely dependent upon the persistence or non-persistence of a macrosporangium, which is always formed. "When a megasporangium has reached the stage in which eight spore mother cells are in synapsis some of the outer cells of the stalk enlarge and become apical cells of the young microsporangia." The eight macrospore mother cells give rise to thirty-two macrospores. If all but one disintegrate, the development of the microsporangia is suppressed. If, on the other hand, all the macrospores disintegrate, the microsporangia continue development, the macrosporangium collapsing and the sorus then becoming a micro-sporocarp. In each microsporangium appear sixteen spore mother cells whose division gives rise to sixty-four spores.

In the further development of a microsporangium, according to Stras-burger (1889), a single tapetal layer is cut off from the central cell and sixteen microspore mother cells are formed by the division of the remaining central cell. The walls of the tapetal cells disintegrate and their protoplasts coalesce as the spore mother cells round up for meiosis. The tapetal plas-modium flows in among the spore mother cells; the contents of the micro-sporangium round up in the center, remaining connected only by thin cytoplasmic plates with the jacket of the capsule. The spore mother cells, apparently separate from one another, divide within this mass, in which the tapetal nuclei are uniformly distributed. The spores grow to their ultimate size and each becomes provided with an exine. The older spores are surrounded by clear areas which swell and coalesce so that finally a number of spores come to lie in a single vacuole; eventually, for each future massula, there is one such group of spores. The vacuole in which each group lies is surrounded and separated by plates of less vacuolate tapetal plasmodium; in consequence of vacuolar growth the sporangium attains its mature size. The plasmodial plates containing tapetal nuclei become thicker and more viscous; within the vacuoles granules derived from the plates appear and coagulate into delicate membranes. These massular membranes increase in thickness through the deposition of more granules; chemical tests show their composition to be similar to that of the walls of spores and pollen grains. The surrounding granular tapetum gives rise to glochidia, whereupon the remainder of this portion of the tapetum and the included leucoplasts disintegrate. The massulae are now mature.

Hannig (1911) found spindle-shaped nuclei in the tapetal plasmodium which he interpreted as representing stages in amitosis, since the number of nuclei increases. He, like Strasburger, considered the membranes of the massulae to be built up in vacuoles containing spores and nuclei by the coagulation of granules derived from the tapetal protoplasm surround-ing the vacuoles. He noted that as the massulae mature the number of

tapetal nuclei diminishes; he gave also an account of the growth of the massulae. Glochidia develop from the exterior membranes of the massulae, while the latter are still lying in vacuoles, as irregular swellings which elongate and develop anchor-shaped heads. The walls of the glochidia become thicker at maturity. The pressure to which they are subjected in the sporangium keeps them prostrate on the surface of the massulae, but when the massulae are freed in water the glochidia spring upright in consequence of the shape of their basal portions. Campbell (1918) remarked that the apparent cellular structure of the massulae is probably the result of vacuole formation. He noticed that tapetal nuclei can be detected on the outside of the massulae almost up to the time of maturity.

Strasburger (1889) accounted for the development of the swimming organs and epispore of the macrospore in *A. filiculoides* in much the same way as for the formation of massulae. The three apically placed swimming organs are constructed of membranes built up in three vacuoles. The membranes of the chambered and warty epispore are similarly built up in small clear areas (vacuoles) oriented radially about the base and sides of the macrospore, which has now grown to fill the lower portion of the sporangial cavity. The whip-like appendages are formed, by the same method as glochidia, from the knobs of the epispore and from the apex of a stalk centrally located between the swimming organs. The chemical reactions of the membranes of the epispore and swimming organs are the same as those of the membranes of the massulae.

Hannig (1911) considered that the three apically placed vacuoles result from the fusion of smaller vacuoles in which the disintegrating macrospores lie, so that each of the three comes to contain approximately the same number of degenerating spores. Within these vacuoles the membranes of the mature swimming organs are built up; at maturity the functionless macrospores appear caught in the meshes of the swimming organs. The functional macrospore, too, lies in a vacuole within which the membranes of the epispore are constructed, so that the epispore plus the macrospore and the three swimming organs with their included functionless macrospores are respectively homologous with massulae. Hannig considered the whip-like appendages to be outgrowths of the surface of the vacuole in which the macrospore lies. Since the tapetal nuclei of both micro- and macrosporangium are passive and have no regular or fixed position, they play no part in the growth of the massulae. The periplasmodium, however, is a living protoplast which determines the location of the inclusions and constructs the epispore in either macro- or microsporangium.

Apparently the only statements in the literature regarding mitosis in *Azolla* are by de Litardière (1921). He observed 48 short chromosomes

in somatic divisions in *A. caroliniana*. In the telophases the chromatic
material flows out from the ends of the chromosomes to form delicate
fibers which anastomose with other similarly derived fibers. The chromo-
somes remain distinct throughout the interphases. In the prophases
there is, first, a continuous spireme; then the anastomoses disappear and
the chromosomes elongate somewhat, assume their characteristic short
rod shape, and become double. The chromosomes then shorten; in the
equatorial plate frequently appear linear series of chromosomes con-
nected by fibers.

MATERIAL AND METHODS

In the present study plants of *Azolla filiculoides* Lam. bearing sporo-
carps collected at Palo Alto, California, and fixed by Dr. D. A. Johansen
have been used. Fixations were made in formalin-acetic-alcohol, chrom-
acetic, and Carnoy's alcohol-acetic fluid (five minutes) followed by
chrom-acetic. Vegetative material of *A. caroliniana* Willd. and *A. filicu-
loides* Lam. growing in the botanical greenhouses of the University of
Wisconsin was fixed in Randolph's, Belling's, and Karpechenko's modifi-
cations of Navashin's fluid, and in Carnoy's alcohol-acetic mixture. For
the study of the cytoplasm Carnoy's fluid followed by chrom-acetic has
been most successful; for nuclei, modifications of Navashin's fluid. Mate-
rial fixed in formalin-acetic-alcohol was used only for morphological
studies.

The material was dehydrated with alcohol or with dioxan. The use of
the latter resulted in less hardening of the mature massulae than did that
of the former. Chloroform or dioxan was used as an infiltrating agent and
a commercial grade of paraffin as an imbedding agent.

Sections were cut from 5 to 15 microns in thickness and stained with
Flemming's triple stain or with Smith's modification of Newton's crystal
violet-iodine. The latter was most helpful in determining the presence of
nuclei at stages when their chromaticity is low, for the study of chromo-
some morphology and number, and for meiosis. By further modifying the
crystal violet-iodine schedule, favorable staining of the tapetal cytoplasm
was possible. For gross morphological study a safranin stain followed
by a wash of dilute fast green was used.

OBSERVATIONS

Development of Sporocarps and Sporangia

In the material studied, sporocarps appear singly or more commonly
in pairs; in no case were more than two observed together. The two of a
pair may be of the same or of opposite "sexes." The sporocarp initial

takes the place of the lower leaf lobe; it has not been observed to dichoto-
mize; it develops by means of an apical cell with three cutting faces, form-
ing a columella. While the columella is still short a collar-like growth, the
indusium or sporocarp wall appears about its base (*i*, fig. 1). By the
time the apical cell has given rise to the columella (*c*) and a macrospo-
rangium, these are surrounded but not closely invested by the indusium.
The hood (*h*, fig. 5) arises from the lower side of the upper leaf lobe and
grows out over the sporocarp.
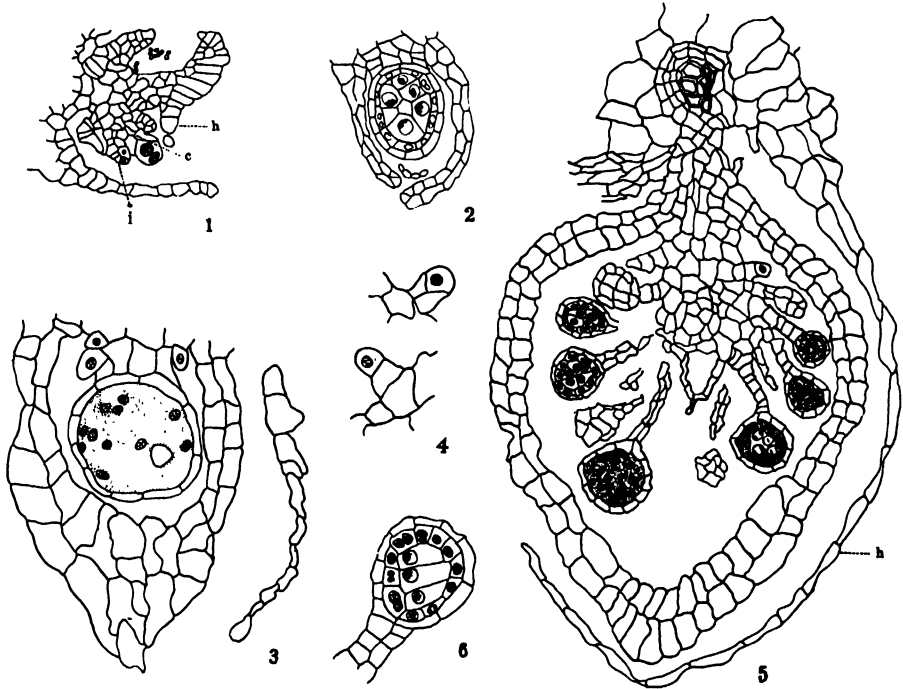
All drawings were made with a camera lucida except those of the microspore mother
cells.

Fig. 1. Longitudinal section of a sporophyll, the hood (*h*), and the sporocarp initial
(*i*, indusium; *c*, columella). ×208.

Fig. 2. Longitudinal section of a young macrosporocarp showing an unelongated
columella and a terminal macrosporangium. ×345.

Fig. 3. Longitudinal section of a macrosporocarp (not median of the distal portion of
the sporocarp wall). The columella is elongated and microsporangial initials are devel-
oped. ×345.

Fig. 4. Longitudinal sections of initials arising from the epidermis of the elongated
columella. ×345.

Fig. 5. Longitudinal section of a young microsporocarp showing a collapsed macro-
sporangium terminal to the columella and the basipetal sequence of microsporangia
(*h* is the hood). ×315.

Fig. 6. Longitudinal section of a microsporangium. The microspore mother cells are
entering synizesis while the tapetal cell nuclei are in the first wave of division. ×345.

Whether a macro- or a microsporocarp is ultimately to develop, a macrosporangium is always formed. The apical cell of the columella becomes the apical cell of the developing macrosporangium so that no more macrosporangia are ever formed (fig. 2). While meiosis is taking place in the macrosporangium the columella elongates and certain of its epidermal cells become the apical cells of microsporangial initials (figs. 3, 4). If, in the developing macrosporangium, one macrospore persists, the rudiments of microsporangia are suppressed; a macrosporocarp develops. If all the macrospores disintegrate, the macrosporangium collapses and the secondary initials below develop into microsporangia; a microsporocarp thus appears. The microsporangia arise in basipetal sequence from the columella, so that in a longitudinal section of a microsporocarp sporangia of various ages appear (fig. 5). As many as 130 microsporangia have been counted in a single sporocarp.

Sporangia of both types are leptosporangiate in origin and development. The stalk of the macrosporangium is short, relatively thick, and difficult to distinguish from the columella (fig. 3). The jacket, one cell thick, is formed by periclinal cell divisions on the anterior and lateral cutting faces of the apical cell; the remaining central cell gives rise to a single tapetal layer by several more periclinal divisions. The centrally located archesporial cell now remaining undergoes a series of three divisions in as many planes which form eight macrospore mother cells. The mature macrosporangium is usually ovate.   .

Each secondary apical cell possesses three cutting faces. In case these cells become active, each gives rise by divisions in its posterior faces to a stalk of two cell rows. The cells of the stalk elongate until complete maturity of the microsporangium. Rather early the apical cell cuts off on its anterior and lateral faces jacket cells; similar periclinal divisions of the central cell give rise to a single layer of tapetum. The remaining central archesporial cell undergoes a series of cell divisions in several planes to form 16 microspore mother cells. The shape of the microsporangium at maturity is spherical.

The divisions of the cells of each successive generation leading from archesporial cell to spore mother cells (five cell generations in the microsporangium, four in the macrosporangium) are simultaneous. Nuclear and cell divisions in the tapetal and jacket cells keep pace with the increase in the circumference of the sporangium up to the time of spore mother cell-formation.

Microsporogenesis and Development of Massulae

During synizesis in the microspore mother cells the nucleus of each tapetal cell divides mitotically so that these cells become binucleate (fig. 6).

In many cases each daughter nucleus divides almost immediately. Nuclear division is not followed by division of the tapetal cells. At about the time of the onset of leptonema in the nuclei of the spore mother cells, the walls of the tapetal cells disappear; their nuclei are now in various stages of a second series of divisions—mostly in the prophases, a few in metaphases and anaphases. Neither the first nor the second series of divisions of tapetal nuclei is perfectly simultaneous; but by the time the spore mother nuclei are in pachynema the tapetal nuclear divisions are completed and the daughter nuclei lie free and greatly crowded in a plasmodium occupying the periphery of the sporangial cavity (fig. 7). The spore mother cells have rounded up by this time, and are aggregated into a roughly spherical group.

When the anaphases of the homoeotypic division have been reached, the spore mother cells lie somewhat apart from one another in the cytoplasm of the tapetal plasmodium which has now begun to invade the central region of the microsporangium (fig. 8). The division of spore mother cells into tetrads is simultaneous and by means of cell plates oriented on spindles between each pair of nuclei (fig. 29).

The microspores become separated from one another and grow to about three times their original diameter. Tapetal nuclei as well as cytoplasm are now present in the central region of the sporangium. The walls of the immature microspores are thin; their protoplasts, as the spores grow, become increasingly vacuolate; the nucleus of each spore is somewhat flattened and lies near one side.

As a spore matures, a smooth wall is deposited. Apparently the wall layers are secreted by the spore protoplast itself, since no coagulation of granules derived from the tapetal plasmodium has been observed. Ultimately the wall consists of an outer relatively thick layer, next a thin darker layer, and within this a third layer somewhat less thick than the first but optically similar. Triradiate ridges are visible on the apical face of each spore at maturity.

After the spores have reached approximately their mature size they pass to the peripheral region of the sporangial cavity. The majority of the tapetal nuclei now lies in the central region (fig. 9). Many of the latter nuclei become spindle-shaped with irregular blunt ends (fig. 10). It is not improbable that cytoplasmic streaming carries many of the nuclei inward and the spores outward, the latter being caught sooner or later in the developing massulae. If so, the spores do not necessarily lie in the peripheral regions as earlier descriptions imply. This seems to be the case, since many of the spores, before their location is finally fixed, are apparently carried back to the center again after migrating to the periphery.

Spores frequently but not invariably seem to lie in vacuoles. A certain amount of shrinkage is to be expected in fixing material like the contents of a sporangium the concentrations of whose component parts vary greatly. The criterion of the efficiency of a fixation has been mainly the plumpness of the tapetal nuclei and the absence of "halos" about the nucleoli. The tapetal cytoplasm at the time of initiation of the massulae is very susceptible to osmotic changes, and the thin, delicate platelets of the massulae are frequently torn and crumpled, although many of the nuclei are plump.

The spindle-shaped nuclei are not fixation artifacts since they occur in the same region of the tapetal plasmodium with typically ovoid nuclei which possess rather evenly dispersed chromatic reticula and intact membranes. The spindle-shaped nuclei are not amoeboid, since their membranes are irregular and fragmentary. In addition, their chromatic networks become irregularly aggregated and their chromaticity increases; it would seem that such nuclei are disintegrating. Upon complete dissolution of the nuclear membrane, the chromatic substance may for a short period retain its stainability. Occasionally clumps of chromatic granules are found, but their infrequent occurrence suggests that the chromatin is rather quickly resorbed. Compression of developing vacuoles at times gives these disintegrating nuclei odd shapes and may cause great elongation.

The disappearance of the tapetal nuclei is haphazard at first but ultimately highly discriminatory, for soon the only ones left are those in the peripheral layer of the tapetal plasmodium and in intersecting plates of less vacuolate cytoplasm extending across the sporangium (fig. 11 A, B). The nuclei in these two regions retain their normal ovoid shape and sparse reticula.

Explanation of Figures 7–11

Fig. 7. Cross section of a macrosporangium. The microspore mother nuclei are emerging from synizesis and the tapetal walls have broken down, allowing the tapetal cell contents to coalesce and form a plasmodium. Another wave of tapetal nuclear divisions follows. ×750.

Fig. 8. Cross section of microsporangium. The microspore mother cells are separating from one another and the tapetal plasmodium is invading the central region of the sporangium. ×690.

Fig. 9. Cross section of a microsporangium. The microspores lie at the periphery while the tapetal plasmodium fills the sporangial cavity. Tapetal nuclei and vacuoles are irregulary distributed. ×690.

Fig. 10. Portion of the tapetal plasmodium. The homogeneous area is in the central region of the microsporangium. The spindle-shaped nucleus and the radially elongated vacuoles and fibers toward the outside are characteristic of the plasmodium in the regions where the massular rudiments develop. ×1975.

Fig. 11. A. Longitudinal section of a microsporangium. The massular rudiments containing spores and the intersecting nucleated plasmodial plates are shown. ×260. B. The platelets of a massular rudiment and an almost entirely disintegrated nucleus within it. × ca. 1000.

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11 B

11 A
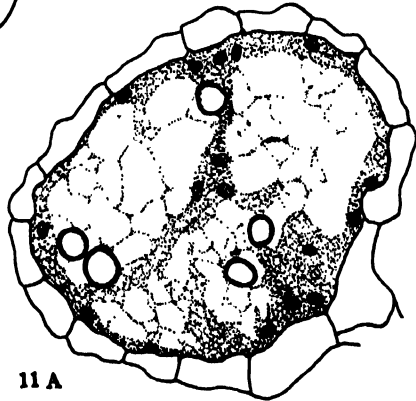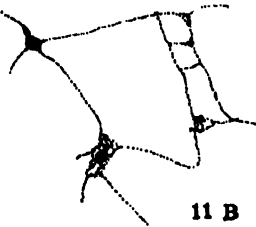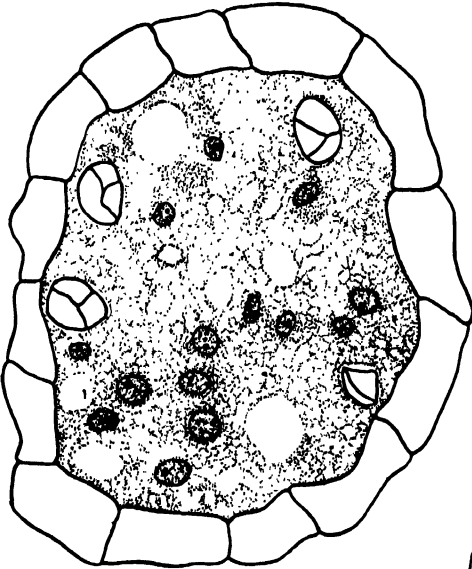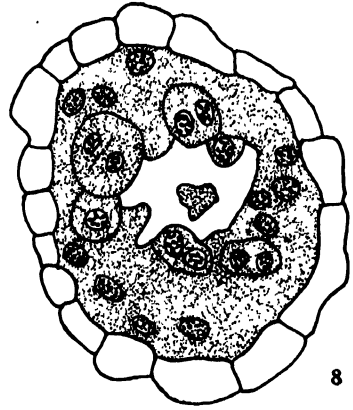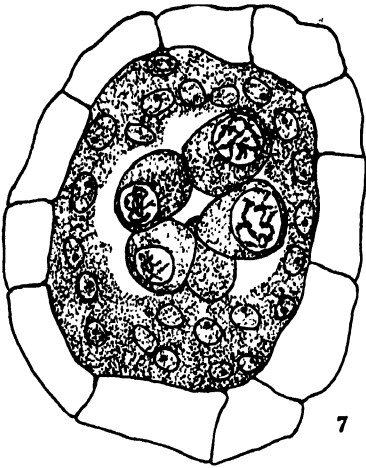
Before the disappearance of any of the nuclei the cytoplasm of the tapetal plasmodium is rather granular, the vacuoles present being small and indiscriminately scattered. While the nuclei are disintegrating, con-
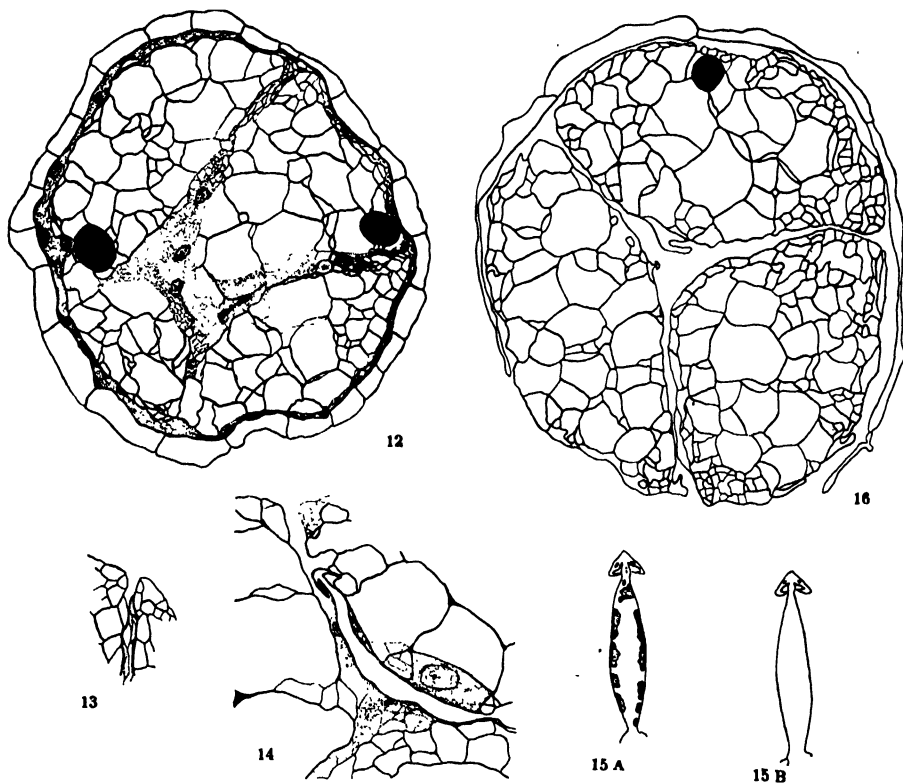
Fig. 12. Cross section of a microsporangium. The massulae are almost mature but are not yet separated. The plasmodial plates are just becoming vacuolate. × ca. 230.

Fig. 13. Portion of a plasmodial plate and massulae. The elongated vacuoles in the former will fuse and provide a means of separating the massulae. ×695.

Fig. 14. Glochidium forming on the inner surface of a massulae in a region where the tapetal plasmodium left is nucleated. ×860.

Fig. 15. Mature glochidia. A is the type described for certain plants; B is the common type. ×494.

Fig. 16. Cross section of a mature microsporangium. Three massulae are present. ×345.

siderable activity of the plasmodium is demonstrated by the arrangement of the granules into rows or into radiating catenate fibers (fig. 10). After the disintegration of the nuclei in the several regions (three to eight), between the intersecting plates in which the tapetal nuclei remain unaffected, the vacuoles of these regions increase greatly in size in consequence of some vacuolar fusion and of an actual increase of sap. The

maximum growth of the microsporangium occurs at this time; the capsule wall becomes greatly distended as vacuolar growth rapidly proceeds.

The from three to eight enucleate and vacuolate regions are rudiments of massulae (fig. 11 *A*). Each includes a variable number of microspores. The staining reaction of the intervacuolar material is slightly changed; it is compressed by the pressure of vacuolar growth into thin platelets in which may be found the remains of disintegrating nuclei (fig. 11 *B*). The delicacy of the platelets is demonstrated by the difficulty encountered in obtaining adequate fixation of the sporangium at this time. Later the platelets become more tenuous and hardened, a condition shown both by plasmolytic methods and by staining reactions; thereafter the vacuoles increase no more in size.

While construction of massulae is proceeding, the nuclei in the cytoplasmic plates separating the massular rudiments are still apparently healthy although they show some loss of chromaticity (fig. 12). When the membranes of the massulae assume their final texture, the nuclei of the plasmodial plates begin to disintegrate; the subsequent vacuolation is somewhat slower and more irregular (fig. 12). The vacuoles enlarging in these intermassular plates are flattened, probably in consequence of compression. The vacuolation of these plates may take place either almost immediately upon maturation of the included massulae or in the course of a relatively long period thereafter—depending upon the persistence or non-persistence of the nuclei. The elongated and flattened vacuoles in the plates fuse and the massulae become separated by a process resembling progressive cleavage (fig. 13). The cleaving process at times leaves a bit of cytoplasm with, usually, an included nucleus lying between the massulae.

As yet there is a complete peripheral sheath of tapetal plasmodium containing intact nuclei. This material and that left between the massulae by the cleaving process is the last active in the sporangium and is responsible for the formation of glochidia. Some of the peripheral layer may flow into the spaces left between the massulae or may remain, for a considerable part, in its original position. Early stages in the formation of glochidia have not been seen; by the time the massulae are separated the glochidia have formed. There is evidence that a nucleus is present at the base of each young glochidium and that the nucleus does not disappear until the glochidium is almost completely formed; there is evidence also that the glochidium is the result of a vacuolation and a constructive deposition of granules derived from the active portion of the plasmodium (fig. 14). Strasburger (1889) and Hannig (1911) described the walls of the glochidia as being of uniform thickness. In this study certain plants have been found all of whose glochidial stalks have walls made up of alternate thick and thin bands on the inner face (fig. 15 *A*); in other plants the

glochidia are of the uniformly thickened type (fig. 15 *B*). Once the glo-
chidia are formed, the massulae are mature (fig. 16). Probably all the
peripheral layer of tapetal plasmodium and any undifferentiated cyto-
plasm which may have remained between the massulae are exhausted in
glochidium formation.

Development of the Macrospore and Accessory Structures

In the macrosporangium the sequence of tapetal nuclear divisions
is similar to that in the microsporangium. The eight spore mother cells,
all of which divide, and later the spores, are separated from one another
by the influx of the tapetal plasmodium as in the microsporangium. The
single macrospore which persists occupies a basal position in the sporan-
gium; its apical faces are usually turned toward the apex of the sporangium
(fig. 17). The macrospores above, although they deposit cell wall mate-
rial, never grow materially and eventually become rather granular. They
do not completely disintegrate, for traces of them may be found at the
maturity of the epispore in the meshes of the swimming organs (fig. 20).

The persistent macrospore grows to occupy most of the lower part
of the sporangium. The wall of this macrospore is constructed in a similar
fashion to that of the microspores, but is thicker and is traversed by
canaliculi of varying diameter (fig. 18). Through these channels there
may well be protoplasmic connections between the spore protoplast and
the tapetal plasmodium, since plates of less vacuolate cytoplasm lie oppo-
site their openings. In the apical region of the sporangium the disintegrat-
ing macrospores are scattered irregularly. These, in consequence of plas-
modial activity, sooner or later come to lie in three groups (frequently
one group opposite each of the three apical faces of the persistent macro-
spore).

In the region of each of these upper groups of macrospores the tapetal
nuclei disintegrate and the plasmodial cytoplasm becomes increasingly vac-

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Explanation of Figures 17–22.

Fig. 17. Semidiagrammatic drawing of a longitudinal section of a macrosporangium
at the time of the initiation of the rudiments of swimming organs toward the distal end
of the sporangium. Note the disintegrating macroscopores caught in the meshes of the
rudiments and the basal functional macrospore. ×690.

Fig. 18. Portion of the lower part of a macrosporangium from the macrospore wall
outward. The vacuolated strips are rudiments of "warts." ×690.

Fig. 19. Portion of the epispore of the macrospore showing the whip-like appendages
arising from the apex of a wart in an area where nucleated cytoplasm is present. ×1780.

Fig. 20. Longitudinal section of a mature macrospore and its appendages. This sec-
tion does not show the attachment of the swimming organs to the columella. ×155.

Fig. 21. Polar view of a somatic equatorial plate. About forty chromosomes can
be distinguished. × ca. 3800.

Fig. 22. Microspore mother nucleus in synizesis. × ca. 3800.

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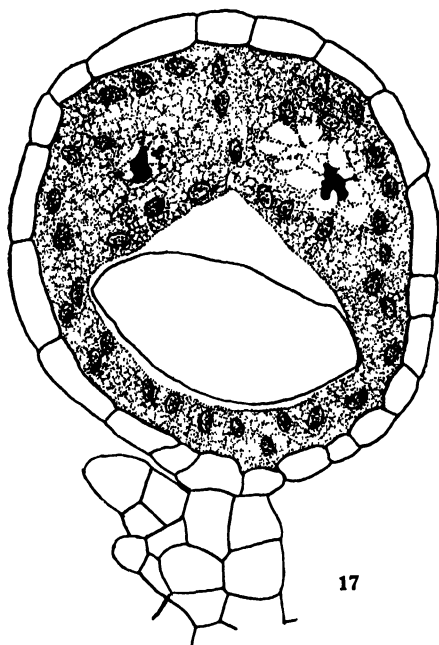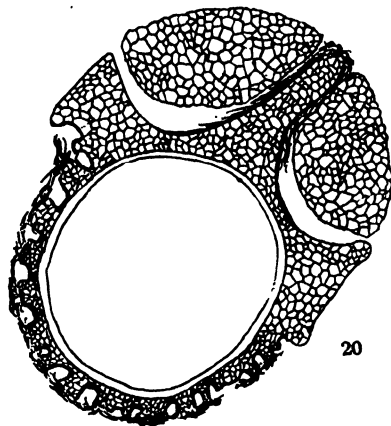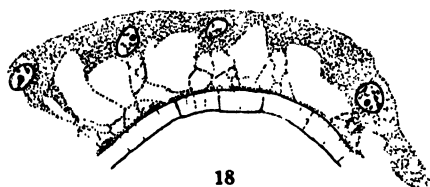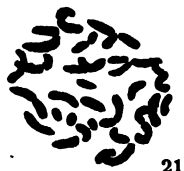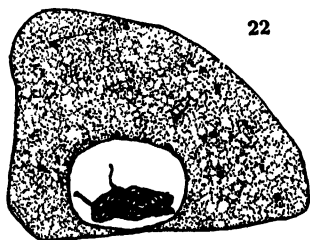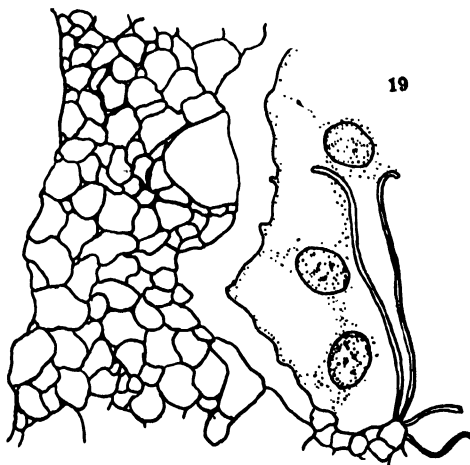
uolate. These regions constitute the rudiments of the three swimming organs
(fig. 17); they are homologous with the rudiments of massulae. The
vacuoles in these regions grow, and the intervacuolar substance is flattened
into thin platelets which are to harden and become parts of the mature
swimming organ. In the region between each two adjacent rudiments, in
a common central region, and in the peripheral region of the upper part
of the sporangium, the tapetal nuclei are still intact and the plasmodium
is active. The nuclei in these plasmodial plates between the rudiments,
between each rudiment and the epispore formed on the macrospore below,
and in the tapetum at the subapical periphery of the sporangium, next
disappear. In each case the cytoplasm left becomes vacuolate and the
intervacuolar substance is transformed into platelets. Those platelets
arising at the periphery of the sporangial cavity are continuous with
those of the initials of the swimming organs. As in the separation of the
massulae, a process resembling progressive cleavage ensues in the areas
between adjacent swimming-organ rudiments and between the initials
and the epispore. In the cleavage zones, because of the compression of
two developing rudiments or of a developing rudiment and the epispore,
the vacuoles become flattened and fuse before the platelets become hard-
ened. The common central region contains active cytoplasm and intact
nuclei. This portion of the plasmodium gives rise at its apex to whip-like
appendages (fig. 20). The remainder of the central region is transformed,
by the disintegration of nuclei, a subsequent vacuolation, and the harden-
ing of the intervacuolar substance, into the platelets of the mature struc-
ture of the columella, to which the swimming organs are attached. Here
there is no fusion of vacuoles at a relatively late stage and no separation
of the swimming organs at their inner faces from the columella or of the
columella from the epispore of the macrospore, so that the three swimming
organs are attached on their inner faces to the columella which, in turn,
projects outward from the spore below.

The epispore is developed in a fashion comparable to the development
of the massulae and swimming organs. The lower part of the sporangial
cavity outside the space in which the macrospore lies is at first filled with
tapetal plasmodium. In plasmodial plates radiating from the macrospore
wall, generally extending from the canaliculi, and in a peripheral sheath
of tapetal plasmodium which is intersected by these plates, the nuclei
remain intact; in the areas bounded by the plasmodial plates, the macro-
spore wall, and the peripheral layer the nuclei disappear and vacuolation
takes place. Upon vacuolation of the plasmodial plates after their nuclei
have disappeared, the intervacuolar substance is transformed into the
platelets of the chambered warts of the epispore (fig. 18). Apparently the
remaining active peripheral portion of the plasmodium may be utilized in

several ways. In regions where the nuclei disappear relatively early, the intervacuolar substance is transformed into platelets—commonly at the apices of the warts of the part of the epispore already formed—or where the nuclei persist for a longer time, the plasmodium gives rise to the whip-like appendages at the apices of the warts (fig. 19) or forms of homogeneous layer in the depressions between them. The construction of the epispore is simultaneous with the formation of the swimming organs, each similar step being coincident in both areas. (Figure 20 illustrates the mature structure.)

Mitosis

Each nucleus of *Azolla* possesses one or two nucleoli, a sparse reticulum, and a large amount of karyolymph. The nuclei of the meristematic cells of root and stem tips and those of the cells of embryonic leaves never completely pass into a typical resting condition. This is true, also, of the nuclei in all regions in which there is rapid and repeated nuclear division, as in the tapetal cells and the sporogenous region. As the cells in root and stem tips and of the leaves approach maturity, and after the cessation of nuclear division in tapetal cells, the chromatic material of the nuclei becomes dispersed into a more or less uniform reticulum.

The interkinetic condition of the actively dividing nuclei is similar to that described by Rosenberg (1904) for certain cells of *Capsella*. Because of the close grouping of the chromosomes at late anaphases and early telophases the origin of the connecting fibers cannot be determined. After the chromosomes have separated somewhat, however, the greater part of the chromatic material forms aggregates equal in number to the chromosomes, connected with one another by fine threads. These aggregations are prochromosomes, or, according to Smith's (1934) interpretation, persistent points of spindle-fiber-attachment of the chromonemata.

In the early prophases the fine connecting threads disappear and the chromosomes elongate somewhat. The nucleolus persists until the chromosomes are fully formed. As the chromosomes pass to the equatorial plate they become greatly shortened. The chromosomes are not uniform in size, but in general they are short and rod-shaped (fig. 21). The equatorial plate is comparatively flat, there being no long chromosomes with trailing arms. In somatic plates the chromosomes have a tendency to be arranged in linear series by fine connecting fibers—evidently not all previous associating connections being lost until the time of the early anaphases. About forty chromosomes may be distinguished (fig. 21).

The separation of the daughter chromosomes is not strictly simultaneous. It is particularly noticeable that one or two pairs of daughter chromosomes migrate toward their respective poles much earlier than

the other pairs. Once their migration has begun, however, the precocious chromosomes lag and the remainder of the daughter chromosomes reach the poles at about the same time as the first to start. The chromosomes are so small that the point of spindle fiber-attachment is not easy to determine; no constrictions are recognizable.

Meiosis

The premeiotic divisions of the sporogenous cell nuclei seem to be similar to other mitoses. The spore mother cells are at first angular in outline; they do not round up until the nuclei are emerging from synizesis (fig. 22). The condition of the spore mother nuclei at the onset of meiosis does not seem notably different from the interkinetic condition of somatic nuclei. There is commonly a single nucleolus and a peripheral reticulum of chromatic material. The reticulum consists of numerous large, deeply staining bodies (the prochromosomes) connected, at least in part, by fine threads. In the early prophases the material on either side of the prochromosomes becomes increasingly chromatic; the time of disappearance of any of the connecting threads could not be determined. The leptotene chromosomes appear as elongated and at times moniliform threads, whose internal structure is indistinguishable. There is some tendency for pairing of certain parts of homologous chromosomes but this tendency does not seem to be carried to any great length. Such preliminary pairing is followed by a complete collapse of the threads into a contracted mass at one side of the nucleus. From this synizetic mass but few thread ends project (fig. 22).

In the cytoplasm of the spore mother nuclei appear irregular granules, which with the crystal-violet iodine technique stain like the chromatic material. These granules are scattered, some of them being close to the nuclear membrane. Since they persist throughout meiosis it seems probable

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Explanation of Figures 23–30

Fig. 23. Microspore mother nucleus in diakinesis. Note fibers connecting some of the pairs.

Fig. 24. Microspore mother nucleus in late diakinesis.

Fig. 25. Metaphase of heterotypic division in a microspore mother cell. Note the fibers attaching the two pairs of smaller chromosomes to two larger pairs. These smaller chromosomes commonly leave the equatorial plate before any of the others.

Fig. 26. Polar view of a heterotypic equatorial plate in a microspore mother cell. The chromosomes pairs cannot be counted with any certainty.

Fig. 27. Nuclei in a microspore mother cell at the completion of the heterotypic division. (Drawings at two different levels.)

Fig. 28. Homoeotypic division in a microspore mother cell. About eighteen chromosomes may be counted in one plate.

Fig. 29. Cytokinesis in a microspore mother cell.

Fig. 30. Tetrad of microspores.
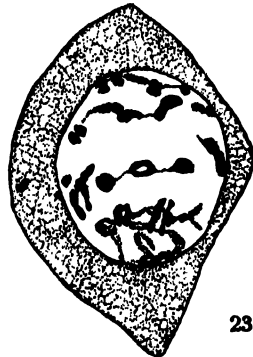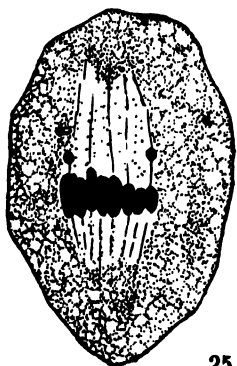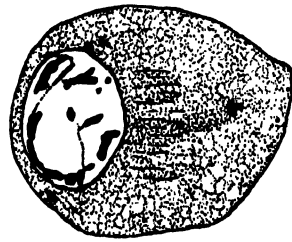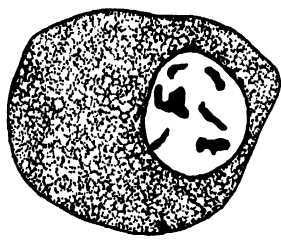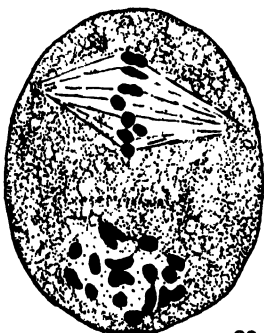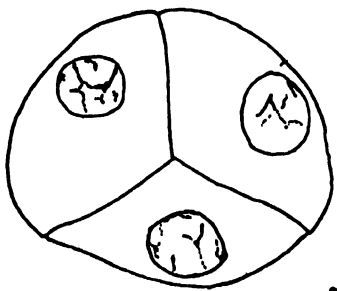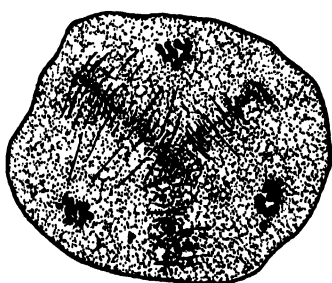
All × ca. 3800.

that they may at times become involved in the spindle; occasionally they are found at the polar regions.

After emerging from synizesis the chromosomes pair so closely that whether or not each chromonema splits at this time cannot be determined. In fact the only evidences of pairing are the decidedly beaded appearance and the evident doubleness of a few free chromosome ends. During the period between diplonema and diakinesis the usual shortening and thickening of the chromosomes takes place. At diakinesis the chromosomes of a pair lie opposite each other, usually partly separated by a narrow clear zone. Each individual chromosome suggests by its moniliform appearance a double nature. The chromosome pairs lies in the peripheral region of the nucleus, occasionally connected with one another by slender fibers (fig. 23).

The chromosomes in the heterotypic equatorial plate are apparently thicker than at the time of diakinesis. Some of the fibers connecting the chromosomes are still evident. Two easily distinguishable pairs of spherical chromosomes are frequently attached to a pair of longer chromosomes so that each pair of longer chromosomes appears to bear a satellite (fig. 25). These same small pairs of chromosomes are the earliest to separate and leave the equatorial plate; the separation may even take place while the spindle fibers are becoming equalized in length. The chromosome pairs are in general closely grouped and occasionally several seem to form continuous chains (fig. 26) ; for these reasons the heterotypic plates are not satisfactory for determining chromosome numbers. The separation of the chromosomes of each pair is, however, regular. Daughter nuclei are reconstituted at the poles; there is little tendency to return to an interkinetic condition (fig. 27). The fibers of the first spindle form at the equatorial region a zone of granules which persists until the homoeotypic metaphase. The homoeotypical equatorial plate provides the most satisfactory place for determining the chromosome number (fig. 28). Counts made at this stage of the haploid number range from 18 to 20. The division of the spore mother cell is simultaneous by means of cell plates on spindles connecting each pair of nuclei (fig. 29).

DISCUSSION

The results obtained in this study indicate, as Strasburger (1873) found, that the sporocarp initial originates by dichotomy of the leaf initial and represents the transformed lower lobe of the leaf. The statement of Goebel (1898) that the sporocarp initial in turn dichotomizes is only indirectly confirmed by the observation of sporocarps in pairs and of their common place of attachment to the stem and their common vascular supply. The hood, as Goebel reported, is an outgrowth from the lower side of the leaf lobe. The sporocarp wall (indusium), in agreement with Strasburger's statement, originates as a collar of cells about the base of the initial.

The findings of Pfeiffer (1907) concerning the method of differentiation of sporocarps are confirmed in all respects. The development of the sporangia is leptosporangiate in type and basipetal in sequence.

The large number of nuclei in the tapetal plasmodium is accounted for by two waves of mitotic divisions: the first, relatively early before the tapetal cell walls break down and while the spore mother cells are rounding up for meiosis, when the tapetal cells become two- to four-nucleate; the second, after the tapetal plasmodium is formed while the nuclei of the spore mother cells are passing from leptonema to pachynema. No tapetal nuclear divisions have been found after the time of diakinesis in the spore mother cell nuclei. No stages in cell division following the first wave of mitoses and no incomplete nuclear divisions have been noted. No amitotic divisions were observed. The illustrations of Pfeiffer's (1907) paper show that she observed binucleate tapetal cells in both micro- and macrosporangia. Hannig's (1911) conclusion, that in *Azolla* the increase in number of tapetal nuclei is through amitosis after the tapetal cell walls have broken down and their protoplasts have united in a plasmodium, is incorrect. Kundt (1910) has found that the tapetal cells of *Salvinia natans*, also in consequence of a mitotic division, become binucleate. The conditions in *Azolla* as to the occurrence and the time of mitotic divisions in tapetal cells are closely in harmony with those described by Cooper (1932, 1933) and Smith (1933), who found that the nuclei of the tapetal layer in the microsporangia of various angiosperms divide mitotically while the microspore mother cells are in synizesis. Cooper (1933) noted that the tapetal cells become two- or, in case of a second mitosis, four-nucleate. Steil (1935) likewise has found nuclear divisions and occasionally incomplete cell divisions in the tapetum of the sporangia of *Ophioglossum* and *Botrychium*.

The results of the present study suggest that the formation of massulae, as well as of the swimming organs and epispore of the macrospore, involves a disintegration of plasmodial nuclei, a subsequent decadence of the plasmodial cytoplasm as indicated by vacuolation, and a direct transformation of the intervacuolar substance into membranes. It seems probable that the massular rudiments are areas wherein metabolic processes such as digestion and water intake are proceeding rapidly. The former process is suggested by the decrease in the amount of granular material in the cytoplasm of the tapetal plasmodium and by the disappearance of the chromatic clumps left by nuclear disintegration. In the strips of cytoplasm stretching across the areas interpreted by Hannig (1911) and Strasburger (1889) as vacuoles, chromatin clumps are still occasionally found. The ordering of the granules into radiating fibers and the increase in size of vacuoles suggest the entrance of water. Both this latter phenomenon and digestion cause much cytoplasmic streaming which in turn determines the location of the spores. The persistence of nuclei in certain areas

of the plasmodium slows down the decadence of the cytoplasm in the spheres of their influence, and any constructive process (such as formation of glochidia and of the whip-like appendages) takes place only in their presence.

Strasburger (1889) approached the problem of the construction of massulae and of the swimming organs and epispore of the macrospore as part of a general study of the growth of cell walls. His interpretation that the spores lie in clear areas, that these areas coalesce, and that the membranes of the various episporic structures are constructed in these areas indicates an attempt to homologize these various processes with the construction about the spores of a "perine."

Hannig (1911) attached more importance to the tapetal plasmodium than did Strasburger, who considered it only as a source of material for membranes. Hannig concluded that this plasmodium has the ability to order the location of its contents, but he too considered that the membranes of the massulae are built up in vacuoles in which granules and nuclei are floating. In this case the intervacuolar material also serves as a source of membrane material. He discounted the importance of the nuclei.

From the results of the present study it appears that the massulae are separated by a process similar to progressive cleavage. The same process partly frees the swimming organs from one another and from the epispore of the macrospore. Separation of the massulae comes about by the utilization of all the material of the plasmodial plates in building up the membranes of the massulae in the areas which the plates separated; consequently nothing lies between the massulae at their maturity.

A new type of structure of the glochidial stalk is described. It seems probable that this structure is not an intermediate stage in deposition of material on the stalk, but rather a variation from the more usual type.

The views herein advanced help to harmonize the massulae, the swimming organs, and the epispore of the macrospore with the homologous structures in *Salvinia*. Heinricher (1882) described the tapetum in that genus as giving rise to an amorphous mass in which the spores are imbedded. Kundt (1910) described the formation of the epispore in *S. natans* as taking place in essentially the same fashion, but in addition he observed that the tapetal nuclei disintegrate just before the vacuolation of the tapetal plasmodium. The condition in *Azolla* is more complicated only in that the tapetal plasmodium gives rise not to a single amorphous mass but to several which may be entirely separated as in the case of the massulae, or only partially so as in the case of the swimming organs and the epispore of the macrospore. Furthermore, the last active portion of the tapetal plasmodium forms the glochidia and the whip-like appendages.

The study of somatic chromosomes has led to results comparable to those of de Litardière (1921). The chromosomes, however, show more variety of shape and length than that author indicates.

Meiosis seems to be typical, although prochromosomes are present in the spore mother nuclei and fibers connect the chromosomes during diakinesis and in the equatorial plates of both heterotypic and homoeotypic divisions. The formation and persistence of such fibers may perhaps be evidence of partial end-to-end (spireme) arrangement of chromosomes in the prophases. The haploid chromosome set is about 20.

SUMMARY

The sporocarp initial replaces the lower lobe of a leaf; the hood is an outgrowth from the upper leaf lobe over the sporocarp. The "sex" of the sporocarp depends on the persistence or non-persistence of a terminal first-formed macrosporangium.

Two waves of mitotic divisions account for the increase in number of tapetal nuclei: first, the tapetal cells become two- or four-nucleate during synizesis in the spore mother cell nuclei; second, after the tapetal protoplasts have coalesced into a plasmodium and before the spore mother cells are in diakinesis, the free-floating tapetal nuclei divide again.

Massular rudiments are centers of cytolysis, related to nuclear disintegration and containing varying numbers of microspores. The intervacuolar material is transformed into the platelets of the massulae. Nucleated strips separating the rudiments meet a like fate. Vacuoles formed therein fuse, providing for the separation of the massulae. Glochidia are formed from nucleated cytoplasm on the massular surfaces.

Swimming-organ rudiments, containing disintegrating macrospores are cytolytic centers off each apical face of the functional macrospore. Separation of these organs from the columella is not realized. Membranes of the warts of the epispore of the macrospore are constructed by vacuolation of radiating strands of cytoplasm. Peripheral nucleated cytoplasm passes into a homogeneous layer in the depressions of the epispore or into whip-like appendages.

In somatic divisions about forty short straight or curved chromosomes appear. Prochromosomes are present in the nuclei of actively growing regions. Strands connecting chromosomes at diakinesis frequently persist until metaphase. Meiosis is typical; from eighteen to twenty pairs of chromosomes can be distinguished. Cytokinesis of the spore mother cells is by cell plates formed on spindles between pairs of nuclei.

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Notes on Alaskan Rust Fungi

J. P. ANDERSON

The writer has been interested in the Uredinales ever since he came to Alaska 25 years ago. During the earlier years specimens were sent to Dr. J. C. Arthur at Purdue University for determination, and reports of these were included in his work on the group in *North American Flora*, Vol. 7, and his *Manual of the Rusts of United States and Canada*. The latter work has been used by the author in determinations of recent collections and the following notes based thereon. In cases where the author was in doubt specimens were sent to Dr. George B. Cummins of Purdue University, Lafayette, Ind., for determination.

SPECIES NEW TO NORTH AMERICA

PUCCINIA ARTEMISIAE-NORVEGICAE Tranz. & Woron. Collected north of the Arctic Circle at Wiseman, August 1, 1939, on *Artemisia arctica* Less.

PUCCINIA GYMNANDRAE Tranz. This species was collected on *Lagotis glauca* Gaertn. on Nunivak Island, July 15, 1938.

SPECIES NOT BEFORE REPORTED FROM ALASKA

UREDINOPSIS STRUTHIOPTERIDIS Störmer, on *Athyrium cyclosorum* Rupr. at Ketchikan, August 4, 1927.

CHRYSOMYXA CASSANDRAE (Peck & Clint.) Tranz., on *Chamaedaphne calyculata* (L.) Moench. at Matanuska and Fairbanks in 1931.

MELAMPSORA ALBERTENSIS Arthur, on *Populus candicans* Michx. at Fairbanks in 1931 and at Wiseman in 1939 on *Populus tremuloides* Michx.

PHRAGMIDIUM ANDERSONI Shear, on *Potentilla fruticosa* L. at Circle, July 19, 1935.

PHRAGMIDIUM RUBI-IDAEI (DC.) Karst., on *Rubus subarcticus* (Greene) Rydb. (*Rubus strigosus* Michx. in part) at Curry, July 22, 1939.

GYMNOCONIA PECKIANA (Howe) Trotter, on *Rubus arcticus* L. at St. Michael and at Stebbins, both near the mouth of the Yukon River, in 1938.

PUCCINIA ARNICALIS Peck was collected in 1939 at Healy and at Wiseman on two different but undetermined species of *Arnica*.

PUCCINIA CONGLOMERATA (Strauss) Schmidt & Kunze, on *Petasites frigidus* (L.) Fries, in the Talkeetna Mountains in 1931 and at Barrow and Wainwright on the Arctic coast in 1939.

PUCCINIA CRUCIFERARUM Rudolphi, on *Cardamine bellidifolia* L. in the Talkeetna Mountains, 1931.

PUCCINIA GIGANTEA Karst., on *Epilobium angustifolium* L. at Circle, July 19, 1939.

PUCCINIA GIGANTISPORA Bubak, on *Anemone globosa* Nutt. at Chitina, July 7, 1935.

PUCCINIA LIGUSTICI Ellis & Everhart, on *Conioselinum Gmelini* (Cham. & Schlecht.) Coult. & Rose on Gull Island in Lynn Canal in 1939, and on var. *kamtschaticum* (Rupr.) Hult. on St. Paul Island in Bering Sea in 1938.

PUCCINIA LINKII Klotz., on *Viburnum pauciflorum* Paylie at Skagway and Matanuska.

PUCCINIA MESOMAJALIS Berk. & Curt., on *Clintonia uniflora* (Schult.) Kunth, at Ketchikan and Hyder.

PUCCINIA OUDEMANSII Tranz., on *Parrya nudicaulis* (L.) Regel at Cape Lisburne, August, 1938. This is a new host, at least for America.

PUCCINIA OXYRIAE Fuckel, on *Oxyria digyna* (L.) Hill near Juneau in 1939.

PUCCINIA POLEMONII Dietel & Holway, on *Polemonium acutiflorum* Willd. at Gambell on St. Lawrence Island in 1938.

PUCCINIA POLYGONI-ALPINI Cruchet & Mayor, on *Aconogonum phyto-laccaefolium* (Meissn.) Small (*Polygonum alpinum* Am. Auth.) at Golovin and Unalakleet in the northeastern Bering Sea region. It was abundant there in 1938.

PUCCINIA PULSATILLAE Kalchbr., on *Pulsatilla ludoviciana* (Nutt.) Heller at Healy in 1939.

PUCCINIA VAGANS var. EPILOBII-TETRAGONI DC., on *Epilobium anagallidifolium* Lam. in the Talkeetna Mountains in 1931.

UROMYCES FABAE (Pers.) de Bary, on *Lathyrus maritimus* (L.) Bigel. at Haines, Matanuska, and Unalakleet, thus extending from southeastern Alaska to the northern Bering Sea.

MELAMPSORA LINI (Pers.) Lév., on *Linum Lewisii* Pursh at Mile 240 on Richardson Highway. This is a little north of the Alaskan Range.

HOSTS NEW TO ALASKA AND EXTENSION OF RANGES

PUCCINIASTRUM PYROLAE (Pers.) Schroet., on *Pyrola minor* L. at Hyder in 1939. Previously reported from Alaska on *Pyrola asarifolia* Michx.

PUCCINIASTRUM SPARSUM (Wint.) Fisch. is reported from Alaska on *Arctostaphylos alpina* L. There is a red-fruited form of the host which has been described by Small as *Arctous erythrocarpa* which seems much more susceptible than the common black species. Collected at several localities in interior Alaska and as far north as Wiseman.

MELAMPSORELLA CERASTI (Pers.) Schroet. is common in the aecial stage on *Picea canadensis* (Mill.) B. S. P. throughout interior Alaska as far north as Wiseman.

MELAMPSORIDIUM BETULINUM (Pers.) Kleb., previously reported on *Betula kenaica* W. H. Evans from southeastern Alaska, was collected at Healy on *Betula glandulosa* Michx. and at Unalakleet on *Betula glandulifera* (Regel) Butler. The last may be a hybrid between *Betula alaskana* Sarg. and *B. glandulosa* Michx.

CHRYSOMYXA PYROLAE (DC.) Rostr. In addition to the hosts reported by Arthur from Alaska this species was collected on *Pyrola chlorantha* Sw. at Matanuska in 1931 and on *Pyrola minor* L. at Valdez in 1935.

MELAMPSORA BIGELOWII Thüm. The uredo and telial forms of this rust are very common on numerous species of *Salix* throughout the territory, but only once did I collect the aecial atage. This was in 1935 on *Larix laricina* (DuRoi) Koch at Mile 287 on the Richardson Highway north of the Tanana River.

MELAMPSORA ARCTICA Rostr. was collected on three additional hosts in 1938: *Salix arctica* Pall. at Point Hope; *Salix glauca* var. *glabrescens* Anders. at Deering; *Salix pulchra* Cham. at Cape Lisburne and at Nome.

TRANZSCHELIA SUFFUSCA (Holway) Arthur was collected at Healy, thus extending its range to central Alaska.

XENODOCHUS MINOR Arthur was collected on *Sanguisorba sitchensis* C. A. Mey. in the Talkeetna Mountains north of Matanuska. Previously reported from America only from Kodiak Island.

PUCCINIA ARENARIAE (Schum.) Wint. was collected on *Merckia physodes* Fisch. at Circle in 1935. This seems to be a new host for America.

PUCCINIA AREOLATA Dietel & Holway was collected on *Caltha asarifolia* DC. at Matanuska and on *Caltha leptosepala* DC. in the Talkeetna Mts. in 1931.

PUCCINIA CORONATA Corda was collected at Wiseman on ? *Calamagrostis canadensis* (Michx.) Beauv. in 1939.

PUCCINIA BISTORTAE (Strauss) DC. was collected at Wiseman on *Polygonum Bistorta* L. in 1939.

PUCCINIA FERGUSSONI Berk. & Br. was collected on *Viola Langsdorfii* Fisch. near Juneau in 1932.

PUCCINIA HEUCHERAE (Schw.) Dietel has been collected on the following additional hosts: *Mitella pentandra* Hook., *Tiarella unifoliata* Hook., and *Tolmiea Menziesii* T. & G. The range extends to the Alaska Peninsula.

PUCCINIA HIERACII (Schum.) Mart. was collected on *Hieracium albiflorum* Hook. at Hyder and on *Taraxacum mutilum* Greene at Fairbanks and at Wiseman.

PUCCINIA MILLEFOLII Fuckel was collected at Healy on *Artemisia elatior* (T. & G.) Rydb. This host is not given among hosts listed by Dr. Arthur.

PUCCINIA ORTONII Jacks. has been collected on *Dodecatheon frigidum* Cham. & Schlecht. in central Alaska, and on *Dodecatheon pauciflorum* (Durand) Greene and *Dodecatheon integrifolium* Michx. in southeastern Alaska. The last host is the same as that given by Arthur under the name *Dodecatheon Jeffreyi* Moore.

PUCCINIA POARUM Niels. The range of this species extends to the Bering Sea and Arctic. Collected on *Petasites frigidus* (L.) Fries on the Pribylof Islands and at Kotzebue.

PUCCINIA PORPHYROGENITA M. A. Curtis was collected on *Cornus suecica* L. at Juneau. This host is not given by Dr. Arthur.

PUCCINIA RETECTA Sydow occurs on the various varieties of *Anemone narcissiflora* L. as far west as Unalaska and to the north of Fairbanks.

PUCCINIA RUBIGO-VERA Wint. var. AGROPYRI (Erikss.) Arth. occurs on *Aconitum maximum* Pall. and on *Thalictrum kemense* E. Fries in the Aleutian Islands. Neither of these hosts is given by Arthur and they do not occur within the range of the rust as given in his manual.

UROMYCES HEDYSARI-OBSCURI (DC.) Car. & Picc. was collected on *Hedysarum Mackenzii* Richards at Wiseman and on an undetermined but different species of *Hedysarum* at Nome and Healy, thus adding two new Alaskan hosts and extending the range to north of the Arctic Circle to the Bering Sea.

UROMYCES PHACAE-FRIGIDAE (Wahl.) Hariot was collected at Eagle Summit on Steese Highway in 1935 and at Wiseman in 1939 on *Astragalus umbellatus* Bunge. This host is similar to if not identical with *Phaca frigida* L. Arthur reports this rust as occurring on *Phaca* sp. on Unga Island, southwestern Alaska; also in northern Europe.

UROMYCES POLYGONI (Pers.) Fuckel was collected at Seward and Palmer on *Polygonum aviculare* L. This extends the range westward.

AECIDIUM GRAEBNERIANUM P. Henn. was collected on a new host, *Limnorchis leptoceratatis* Rydb. This collection was made near Juneau.

<div align="center">SUMMARY</div>

·In this paper two species of rust fungi are reported as new to North America, 22 as not before reported from Alaska, 19 as occurring on 28 host species not previously reported as infected in the territory. In addition the known range of 13 species is extended.

JUNEAU, ALASKA

Notes on Plants of the Pacific Islands—II

F. R. FOSBERG

The second paper of this series deals mainly with the Rubiaceae collected by Dr. Harold St. John in Fiji in 1937. The two regions visited, the wet central plateau of Viti Levu, and the Yasawa group of small islands, have not been explored previously by a botanist, so it seems worth while to record even the common species found there. Two new species are described in *Psychotria* and a new variety each in *Hedyotis, Ophiorrhiza*, and *Gynochthodes*. In addition to Rubiaceae, a new species is presented in *Phaleria* (Thymeleaceae) and two new combinations in *Diospyros* (Ebenaceae). The abbreviations (Ho), (Gr), and (NY) refer to the B. P. Bishop Museum, Honolulu, the Gray Herbarium, and the New York Botanical Garden, respectively, to which institutions I wish to express my thanks for the privilege of studying the material cited.

DIOSPYROS

DIOSPYROS FERREA (Willd.) Bakh. var. NANDARIVATENSIS (Gill.) Fosberg. Caroline Is., Yap: Kanif, *Takamatsu 1966* (Ho); Takiol, *Takamatsu 1835* (Ho).

DIOSPYROS FERREA (Willd.) Bakh. var. **palauensis** (Kanehira) Fosberg, comb. nov. *Maba palauensis* Kanehira, Bot. Mag. Tokyo 48: 405. 1934.

Palau Is.: *Kanehira 499, 556, 406* (leaves narrow), *513* (all NY); Aimiriik, *Kanehira 2339* (NY) (cotype), *Nisida (Kanehira's?) 2479* (NY) (isotype); Garasumao, *Takamatsu 1577, 1560* (Ho).

Differs from var. *littorea* in the slight rusty appressed pubescence on the young growth, and in the large, oblong-elliptic or somewhat obovate leaves with acutely contracted bases and heavy petioles. The leaves are up to 15 cm. long, 8 cm. wide, acuminate, coriaceous, glabrous or very early glabrate; fruit almost spherical, lightly appressed-pubescent, fruiting calyx somewhat cupulate, glabrate outside, tube sericeous inside.

DIOSPYROS LATERIFLORA (Hiern) Bakh. Fiji: Yasawa Group, Waya Island, Nagua, alt. 1300 ft., *St. John 18167* (Ho). Native name *bamba;* fruit edible.

DIOSPYROS SAMOENSIS Gray, Proc. Am. Acad. 5: 326. 1862. *Diospyros vitiensis* Gillespie, Bishop Mus. Bull. 74: 14. 1930. Tonga Is.: Eua, Liku Terrace, *Parks 16321* (Ho).

Bakhuizen (Bull. Jard. Bot. Buit. III, 15: 225–226. 1938) with some doubt reduces both *D. vitiensis* Gillespie and *D. longisepala* Gillespie to

synonymy with *D. samoensis* Gray. This seems correct for *D. vitensis*, but the narrow calyx lobes and flat calyx disk seem sufficient to separate *D. longisepala* as a variety.

DIOSPYROS SAMOENSIS Gray var. **longisepala** (Gill.) Fosberg, comb. nov. *Diospyros longisepala* Gillespie, Bishop Mus. Bull. 74: 14. 1930. Fiji: Yasawa Group. Waya Island, north of Yalobi, woods along Olo Creek, alt. 800 ft., *St. John 18121* (Ho) (differs from Gillespie's description in having slightly longer sepals, slightly shorter seeds, and broader leaves with a rounded base).

PHALERIA

Phaleria ixorioides Fosberg, sp. nov. Arbor parva glabra; folia oblonga vel ovato-oblonga apice acuminata basi cordata subsessilia, petiolo crasso 2–3 mm. longo, costa basi crassa; bracteae late cordatae 1 cm. latae 7 mm. longae, membranaceae; flores albi 5 cm. longi extus glabri intus sericeo-villosi, lobis 4, subpatentibus, 6 mm. longis; gynaecium glabrum 4 cm. longum, squamis obtusis.

Small tree 5 m. tall, trunk 3 cm. thick, vegetative parts glabrous, internodes terete, wrinkled when dry, elongate; leaves oblong or ovate-oblong, apex acuminate, base cordate, subsessile, chartaceous, petiole 2–3 mm. long, very thick, base of midrib also thickened, blade up to 18 cm. long, 7 cm. wide, usually 10–15 cm. long; bracts subtending flower head broadly cordate, obtuse, about 1 cm. wide, 7 mm. long, membranous; flowers white, fragrant, about 9 in a head, peduncle about 1 cm. long; perianth 5 cm. long, glabrous externally, silky-villous internally, tube gradually enlarged upward to 3 mm. wide, lobes 4, ovate, somewhat spreading, 6 mm. long; anthers 8, oblong, in two sets of 4 each, the upper inserted in throat, the lower about 4 mm. below throat; pistil glabrous, 4 cm. long, stigma 5 mm. long, enlarged, spindle-shaped, style fili-form, ovary cylindrical, 1.5–2 mm. long, scales broad, obtuse; fruit not avail-able.

Fiji: Yasawa Group, Waya Island, north of Yalobi, woods along Olo Creek, *St. John 18123* (Ho) (type).

Native name *tarutaru*, "used medicinally for scabies."

Related to *P. pulchra* Gillespie, resembling it in general appearance, but larger-leafed, with smaller bracts and white flowers 5 cm. long. Strik-ingly similar, in general appearance, to certain species of *Ixora*, hence the name.

BADUSA

BADUSA CORYMBIFERA (Forst.) Gray. Fiji: Yasawa Group, Waya Island; Nagua, *St. John 18163, 18099* (Ho); Nakawa Gulch, w. side Batinareba, *St. John 18133* (Ho).

DOLICHOLOBIUM

DOLICHOLOBIUM MACGREGORI Horne ex. Bak. Fiji: Viti Levu, Tholo East, Wainimala Valley, Wainamo Creek, Matawailevu, alt. 1600 ft., *St. John 18219* (Ho).

NEONAUCLEA

NEONAUCLEA VITIENSIS Gillespie. Fiji: Viti Levu, Tholo East, Wainimala Valley, south of Matawailevu, alt. 800 ft., *St. John 18375* (Ho).

This species should be further investigated. The specimen cited above, though with only old shattered inflorescences, shows that the fruits were pedicellate, a fact not mentioned in Gillespie's description.

HEDYOTIS

HEDYOTIS AURICULARIA L. var. **melanesica** Fosberg, var. nov. Caulis adpresso-pubescens glabratus; folia lanceolata acuminata breve petiola, 6–8 cm. longa, 1.5–2.5 cm. lata.

Stems appressed-pubescent, glabrate; leaves lanceolate or elliptic lanceolate, acuminate at apex, acute at base, 6–8 cm. long, 1.5–2.5 cm. wide, shortly petioled; stipules pectinately cut, hirtellous; inflorescences axillary, few flowered (3–10), not strongly congested but fusing to present the appearance of a whorl; corolla white; fruit 1.5–2 mm. long, calyx lobes erect, 1.5–2 mm. long in fruit, apex of fruit not strongly umbonate, fruit apparently indehiscent.

Fiji: Kandavu, hills above Namalata and Ngaloa Bays, alt. 200–400 m., *A. C. Smith 157* (NY) (type). Viti Levu, Tholo East, Wainimala Valley, Matawailevu, alt. 1600 ft., *St. John 18281* (Ho). Without loc., *U. S. Expl. Exp.* (NY). New Hebrides: Eromanga, Dillon Bay, alt. 400 m., *Kajewski 352* (NY).

Probably common in New Caledonia, though I have seen no specimens. Approached by certain Malaysian specimens, but on these the pubescence is more abundant and not so strongly appressed.

This variety is probably the plant Guillaumin (Not. Syst. **3**: 160–161. 1915) had in mind as *Oldenlandia crataegonum*, based on *Hedyotis crataegonum* Spreng. However, in the same publication he demonstrated that the latter was based on a Rumphian plant which Merrill (Int. Rumph. Herb. Amb. 479, 1917) shows to be *H. verticillata* (L.) Lam., a different species, and on a plant from Isle of France (Madagascar), which is a *Spermococe* or something of that affinity, having only one seed in a cell. Therefore the specific epithet *crataegonum* can have nothing to do with the Melanesian plant. This variety is close to two forms found in southeastern Asia and Malaysia, which, though having large leaves similar to those of var. *melanesica,* have, in one, spreading pubescence, and in the other greatly congested, multiflorous inflorescences.

According to St. John, a decoction of the leaves is used in Fiji as medicine for headache. Native names: *poroporo-i-langi* (Fiji), and *noo-lay-yelong* (Eromanga).

HEDYOTIS FOETIDA (Forst.) J. E. Smith in Rees Cyclop. 17, pt. 2, 1811. *Oldenlandia imberbis* Guillaumin, Not. Syst. 3: 161, 1915.

Examination of specimens from New Caledonia: without locality, *Franc 3074* (NY); Mts. of Gatope, *Vieillard 2711* (Gr), the former determined as *O. imberbis* by Guillaumin; shows that they are identical with the widespread *H. foetida*, extending the known range of that species to New Caledonia.

OPHIORRHIZA

OPHIORRHIZA LEPTANTHA Gray, Proc. Am. Acad. 4: 312. 1860. *Ophiorrhiza laxa* Gray, l. c.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubololo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18328* (Ho).

Gillespie (B. P. Bishop Mus. Bull. 74: 26–27. 1930) united these two species. This is probably correct, but the striking variability in such characters as shape of inflorescence, length of pedicels, number of flowers, etc., suggests that there may be subspecific entities present in the species. One of these that seems obvious, even in the absence of much material, is described below.

OPHIORRHIZA LEPTANTHA Gray var. **yasawana** Fosberg, var. nov. Folia membranacea, elliptica, 3.5–5 cm. longa, 1.5–2 cm. lata, integra ciliata; cyma gracilis, pauciflora, 3–4 cm. longa, 2–4 cm. lata; calycis lobi subulati.

Plant slender, about 4 dm. tall; leaves membranous, elliptic, 3.5–5 cm. long, 1.5–2 cm. wide, base acute or slightly attenuate, apex usually slightly acuminate, margin ciliate, strictly entire; inflorescence slender, few flowered, 3–4 cm. long, 2–4 cm. across, calyx lobes subulate, 1.5–2 mm. long; corolla lobes white, tube purple, corollas immature, probably to be rather smaller than in other forms of *O. leptantha*.

Fiji: Yasawa Group. Waya Island, woods along Olo Creek, north of Yalobi, alt. 800 ft., *St. John 18126* (Ho) (type).

Differs most conspicuously in the slender habit and small thin leaves with entire margins (rather than irregular as in most species of *Ophiorrhiza*, including *O. leptantha*).

Native name *karaua*.

MUSSAENDA

MUSSAENDA FRONDOSA L. Fiji: Yasawa Group, Waya Island, Yalobi, alt. 200 ft., *St. John 18008* (Ho).

CANTHIUM

CANTHIUM ODORATUM (Forst.) Seem. Fiji: Yasawa Group, Waya Island, Nagua, alt. 1200 ft., *St. John 18101* (Ho).

GYNOCHTHODES

GYNOCHTHODES OVALIFOLIA (Val.) Kanehira var. **Smithii** Fosberg, var. nov. Fructus magnus, compositus, 2–3 adnatus.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Matawailevu, alt. 2200 ft., *St. John 18298* (Ho) (type). Vanua Levu: Mbua, Lower Wainunu River Valley, alt. 0–200 m., *A. C. Smith 1716* (NY). Fulanga, 0–80 m., *A. C. Smith 1127* (NY).

Differs from the typical form from Micronesia (and Samoa) in the ordinarily much larger fruit, usually composed of two or three fused ovaries, though not invariably so. Single-ovaried fruits are not significantly different from those of plants from Micronesia and Samoa. The only compound ovary observed on material from outside Fiji was a single triple ovary on *Christophersen 2827* from Samoa, on which plant all the other ovaries are simple. In the compound ovaries, the individual ovaries are ordinarily arranged in a straight line, each contributing four cells (some usually abortive), forming two parallel rows. The fruit is oblong in transverse section.

Named for Dr. Albert C. Smith, of the New York Botanical Garden, botanical explorer of the Lau Islands and other parts of Fiji.

Native name *wa thoro;* "fiber used to tie home timbers together," according to St. John.

TIMONIUS

TIMONIUS AFFINIS Gray, Proc. Am. Acad. 4: 26. 1860. *Timonius sapotaefolius* Gray, l. c.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18339* (Ho).

These two plants seem to differ only very slightly, judging from the descriptions. A collection from Ovalau, vic. Levuka, *Gillespie 4468* (NY) may represent *T. sapotaefolius*. It is very similar to the rest of the material of this common species, except that the secondary veins are more or less obsolete. (My use of the term secondary veins corresponds to Gray's primary veins.) This seems to be the principal difference brought out by Gray. The closest relative of this species is apparently *T. Ledermannii* of Ponape, Caroline Islands.

MORINDA

The Fijian species of the *Morinda umbellata* relationship are not well understood, more material and especially field study being required. The identifications given here are to be considered tentative, with some explanation given with the two doubtful ones.

MORINDA BUCIDAEFOLIA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, south of Matawailevu, alt. 1600 ft., *St. John 18241* (Ho).

Here taken to be the liana with elliptic to obovate, obtuse or rounded, reticulate leaves, with few secondary veins, fruits 1 cm. or less across, 4–7 at terminal node.

MORINDA FORSTERI Seem. Fiji, Yasawa Group, Waya Island: Nakawa Gulch, west side of Batinareba, alt. 600 ft., *St. John 18139* (Ho) ; north of Yalobi, woods along Olo Creek, alt. 800 ft., *St. John 18125* (Ho).

MORINDA MYRTIFOLIA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, Matanatavo, head of Wainisavulevu Creek, alt. 3500 ft., *St. John 18309* (Ho).

Here taken to be the liana with small, elliptic, acute or slightly acuminate, chartaceous leaves, internodes 1–2 cm. long, heads few-flowered, 4–6 terminally, flowers white, bearded in throat.

ABRAMSIA

ABRAMSIA TRICHOTOMA Gillespie. Fiji: Viti Levu, Tholo East, Wainimala Valley, Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2600 ft. *St. John 18225* (Ho).

IXORA

IXORA VITIENSIS Gray. Fiji, Yasawa Group, Waya Island: Nagua, alt. 1300 ft., *St. John 18154* (Ho) ("flowers white" but dried red), *18118* (Ho) ("fruit black, globose") ; Naruarua Gulch, west side of Batinareba, *St. John 18047* (Ho) ("fruit black") ; Nakawa Gulch, west side of Batinareba, alt. 800 ft., *St. John 18140* (Ho) ("flowers white, pink-tipped in bud; fruit black").

The variation in this species is perplexing, but more collections are necessary for a better understanding of it.

PSYCHOTRIA

PSYCHOTRIA CARNEA (Forst.) A. C. Smith. Fiji: Viti Levu, Tholo East, Wainimalu Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18340, 18327, 18318* (Ho).

Psychotria chrysophylla Fosberg, sp. nov. Arbor, ramulis glabris; folia oblonga, subcoriacea, glabra, petiolata; stipulae tenues, oblongae, 5 mm. longae, caducae, glabrae, non connatae; cyma terminalis, breve virido-brunneo-pubescens, pentachotoma; calyx infundibuliformis, 11–12 mm. longa, tubo extus pubescente, intus glabro, lobis extus vix pubescentibus; antherae 2.5 mm. longae, basifixae; stylus filiformis glabrus bifidus, corollae subaequalis.

Tree 7 m. tall, trunk 2 dm. through; branches terete, dark gray, glabrous, with short internodes; leaves oblong, blades up to 10 cm. long, 8.5 cm. wide, usually somewhat smaller, apex bluntly acute to very slightly acuminate, base obtuse or rounded to (rarely) acute or attenuate, subcoriaceous, glabrous, secondary veins widely divergent, prominent, 10–12 pairs, petiole 0.5–1 cm. long; stipules thin, oblong, acute or divided at apex, about 5 mm. long, caducous, glabrous, not connate or sheathing; inflorescence a single terminal long- pedunculate cyme, 5–7 cm. long, 4–6 cm. wide, shortly greenish- to brownish-pubescent, peduncle 3–3.5 cm. long at anthesis, pentachotomous, each branch trichotomous to pentachotomous, each branchlet bearing 2–3 subsessile or shortly pedicillate flowers; calyx funnel-form, 2.5 mm. long, with 4 short lobes, ciliate, soon reflexed or revolute, rounded or acutish, the whole pubescent outside; corolla tubular-funnelform, up to 11–12 mm. long, tube pubescent outside, glabrous inside, 8 mm. long, enlarged above, lobes 2.5 mm. long, 0.8 mm. wide, oblong, slightly pubescent outside, erect or ascending; anthers linear, 2.5 mm. long, basifixed, attached in throat; style filiform, glabrous, subequal with corolla, upper 1.2 mm. bifid into divergent, flattened lobes; fruit unknown.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18344* (Ho) (type). Grows in swampy rain-forests.

Native name *thauthau ni viti;* "decoction of leaves used as cough medicine."

Named from the yellow-green color of its leaves when dried, rather unusual in *Psychotria.*

Allied to *Psychotria vomensis* Gillespie but differing in the frequently uncut stipules, in the size, form, and pubescence of the inflorescence, the size and pubescence of the calyx, with its short reflexed lobes, and the externally pubescent corolla, with its oblong lobes.

Psychotria St.-Johnii Fosberg, sp. nov. Arbor, ramulis fistulosis tomentosis; folia chartacea acuminata valde albo-reticulata venulosa; stipulae calyptratae caducae valde rufo-tomentosae; cymae 3–4, graciles, laxae; calyx campanulata, albo-venulosa, 1 mm. longa, 2.5 mm. lata, vix lobata, glabra, in fructubus persistens; corolla hypocraterimorpha, alba, extus glabra, fauci barbata, lobis oblongis reflexis; antherae exsertae subbasifixae stylus glaber corollae

subaequalis supra incrassatus bifidus, frustus ovoideus irregularis, 6.5 mm.; longus, 3.5 mm. latus.

Tree 7–8 m. tall, branchlets fistulose, dark brown tomentose; leaves elliptic to oblong or slightly obovate, apex strongly acuminate, base acute to attenuate, blade as much as 23 cm. long, 9.5 cm. wide, usually much smaller, chartaceous, conspicuously white-reticulate venulose, main veins somewhat brownish pubescent beneath, especially when young, petioles variable in length, 1–4 cm.; stipules calyptrate, up to 3.5 cm. long, densely rusty-tomentose, caducous; cymes borne terminally in 3's or 4's which soon become lateral by development of a bud at the same node, thinly pubescent, peduncle slender, 2.5–3 cm. long, loosely branching several times dichotomously to tetrachotomously, ending in flowers on slender pedicels; calyx campanulate, white-reticulate-venulose, about 1 mm. long, 2.5 mm. broad, very shortly and very obtusely lobed, glabrous, persistent in fruit; corolla salverform, white, tube 3–5.5 mm. long, glabrous outside, throat strongly bearded with coarse white hair, lobes 5, oblong to oblong-ovate, about 2.5–3.5 mm. long, becoming reflexed, glabrous; anthers oblong or narrowly so, about 1.3 mm. long, exserted on filaments 2 mm. long, attached near the base, but sacs somewhat prolonged below attachment, inserted in corolla throat; style glabrous, subequal with corolla tube, thickened somewhat upward, the top 1.5 mm. divided into subulate lobes, disk much raised, fleshy; fruit irregularly ovoid when dry and not quite mature, about 6.5 mm. long, 3.5 mm. broad, pyrenes more or less tricarinate with middle keel strongest, keels somewhat broken, crowned with persistent calyx.

Fiji, Viti Levu, Tholo East, Wainimala Valley: Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2500 ft., *St. John 18284* (Ho) (type); Raradawai, Wainamo-Wainisavulevu divide, alt. 2500 ft., *St. John 18279* (Ho); same loc., alt. 2800 ft., *St. John 18275* (Ho). Growing in moist woods to rain-forests.

Native names: *lewalekaleka, kali, aroasawa.*

Allied to *Psychotria taviunensis* Gillespie, but more pubescent, leaves cuneate-contracted at base, not so strongly acuminate, flowers larger, calyx campanulate, white-venulose, inflorescences more slender, longer. The fruit looks like that of *Psychotria carnea* but smaller. The calyx evidently represents an intermediate step towards that of A. C. Smith's genus *Calycodendron*.

PSYCHOTRIA SERPENS L. Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18343* (Ho).

PSYCHOTRIA TEPHROSANTHA Gray. Fiji, Tholo East, Wainimala Valley: Raradawai, Wainamo-Wainisavulevu divide, alt. 2500 ft., *St. John 18280* (Ho); Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2600 ft., *St. John 18306* (Ho).

The latter specimen is described as a vine 8 m. long, climbing over trees, while the former is described as a shrub 7 m. tall.

PSYCHOTRIA TURBINATA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, Raradawai, Wainamo-Wainisavulevu divide, alt. 2800 ft., *St. John 18267* (Ho).

CALYCODENDRON

CALYCODENDRON MAGNIFICUM (Gill.) A. C. Smith. Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18329* (Ho).

CALYCOSIA

CALYCOSIA PETIOLATA Gray. Fiji, Tholo East, Wainimala Valley: Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18326* (Ho); Wainamo Creek, Matawailevu, alt. 1600 ft., *St. John 18217* (Ho).

CORRECTION:—In my recent paper *Notes on Polynesian Grasses* (B. P. Bishop Mus. Occ. Pap. **15**: 37–48, 1939) on page 46 in the synonymy of *Digitaria stenotaphrodes* Greek letter ϵ should be substituted for ξ, thus disposing of *Syntherisma pelagica* var. ϵ F. Brown. This typographical error was kindly called to my attention by Dr. H. St. John.

ARLINGTON, VIRGINIA

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Mention the BULLETIN

Aphyllous Forms in Pyrola ·

W. H. CAMP

(WITH FOUR FIGURES)

It is the peculiar fortune of certain groups of plants to be more or less constantly worked over by the professional classifier who hopes, presumably, to disentangle their increasingly involved nomenclature and, at the same time, bring the taxonomy of each to an actual representation of its phyletic pattern. One of these is the Pyrolaceae. Between the years 1814 and 1857 the Linnaean genus *Pyrola* had, by gradual attrition, been broken into about a dozen genera, five of which were recognized for North America by Rydberg (1914). A discussion of the merits of these segregate genera is outside the scope of this note, but there is no doubt that well-marked groups do exist. The only question is whether we shall disregard the meaning of the word genus and be "conservative" in our names, or whether we shall recognize that a genus is a *kind* of plants, the word "kind" in this instance referring to those species having in common the particular morphological structures which are used to differentiate the various groups at the present time. Much as I dislike such names as *Erxlebenia* Opiz, I am sympathetic with the narrower definitions of these genera, and can only hope that such further oddities as *Pseva* Raf. continue to remain buried in synonymy.

In spite of my personal tendency toward more narrowly defined genera in the Pyrolaceae, I am inclined toward a broader definition of species than is, at present, in favor with many workers. Too much time, I think, has been spent on the traditional treatment of the species of this group as they are found in herbaria, and too little attention given to the plants as they occur in the field.

One thing of which the student must never lose sight is that the Pyrolaceae are on the physiological borderline between autophytism and parasitism. It is common for authors to refer, for example, to the Monotropaceae and certain members of the Pyrolaceae as "saprophytes." This is

probably not their true status. Nutritionally, at least, they appear to be parasites, deriving their food from the fungous mycelia associated with their roots. The fungus is the saprophytic organism. It is not known what advantage, if any, the fungus gains from this association.[1]

Some years ago it was my good fortune to be able to observe various species of *Pyrola* of western North America in the field. Among these was *P. picta* Smith. Mention of this species immediately brings up the ever-present question of the status of *P. dentata* Smith. Here are a couple of species so loaded down with synonyms, combinations and recombinations that, nomenclaturally, they are becoming a taxonomic burden. If we refer to Andres' (1914) definitive study of this group of species, we note that he has resolved the problem of his subsection SCOTOPHYLLA in somewhat the following manner (the numerous synonyms being omitted):

Pyrola picta Sm.
    subsp. *picta* H. Andr.
        the typical form and:
        var. *sparsifolia* (Suksd.) H. Andr.
        var. *Suksdorfii* H. Andr.
    subsp. *pallida* (Greene) H. Andr.
        the typical form and:
        var. *chimoides* (Greene) H. Andr.
    subsp. *dentata* (Sm.) Piper, apud H. Andr.
Pyrola aphylla Sm.
    the typical form and:
        var. *paucifolia* Howell.
        forma *ramosa* H. Andr.
        var. *leptosepala* Nutt.

The above is, to the taxonomist, an intriguing set of nomenclatural pigeon-holes and might possibly have appeared to be called for on the basis of the 50-odd cited specimens then at the disposal of the monographer.

[1] In this connection, I should like to raise the question: Is there any authentic example of a spermatophyte being, of itself, truly saprophytic? The non-green Orchidaceae, Orobanchaceae, etc., superficially appear to be parasites, some on fungi, others on their chlorophyll-bearing hosts or, as I suspect of our common eastern beech-drops (*Leptamnium virginianum*), dependent on a combination of both. However, in many of the Ericales at least, it is possible that, in the past, the fungous symbionts derived certain vitamins necessary for their growth and development from their chlorophyll-bearing associates, just as many mycorrhizal organisms do today. Gradually, then, through evolution, the spermatophytic members of these associations lost their ability to synthesize chlorophyll and became more and more dependent on the fungi for their basic food materials. Even so, it is not necessary to assume that the spermatophytes have lost the ability to synthesize these same vitamins, still necessary to the life of the fungi, or to assume that the symbiotic relation beween the organisms has been completely eliminated; only that the basic nutrition of the spermatophytic members of the associations has been shifted. My own field observations, however, lead me to believe that

Previously, Piper, in his flora of Washington (1906, p. 434), had listed *P. aphylla* Sm., *P. picta* Sm., *P. picta dentata* (Sm.) Piper, and *P. picta integra* (A. Gray) Piper, with *P. pallida* Greene and *P. sparsifolia* Suksdorf as synonyms of var. *integra*. Contemporaneously with Andres' work, Rydberg (l. c.), who was never overly conservative in his interpretations, was able to recognize only three species in this complex; *P. aphylla* Sm., *P. picta* Sm., and *P. dentata* Sm. One year later, Piper and Beattie (1915) dismissed the problem by saying (p. 275): "Allied to *P. dentata* and *P. picta* is a group of puzzling forms which represent different degrees of saprophytism rather than specific distinctions." Here, and in a subsequent paragraph, was, I think, a clear indication that the biology of the organisms of this group must first be understood before their nomenclature can be clarified. They, of course, traditionally recognized *P. aphylla* as distinct.

If one were to judge solely from the literature and its involved synonymy (not here completely listed), it would seem that *Pyrola picta* and *P. dentata* were the principal species involved in this tangle. There is, however, another and related form which must be considered with them. It is the aforementioned *Pyrola aphylla* Smith.

Aside from one synonym, several so-called varieties, and one form, the nomenclature of *P. aphylla* has remained clean. This would seem to indicate that its delimitation has given previous students of its taxonomy almost no trouble. On the other hand, the variety *P. aphylla* var. *paucifolia* Howell [= (?) var. *foliosa* H. Andr.], should at least have raised certain biological queries concerning the taxonomic status of *P. aphylla* (sensu stricto). This problem was brought to my particular attention when, in Oregon in 1932, I collected authentic *P. picta* and what appeared to be *P. aphylla* on two branches of the same rhizome (near Prospect, Jackson County, *Camp 57*; figure 2). The same locality yielded authentic *P. aphylla* (*Camp 63*). Later the same year along Tahoma Creek, Mt. Rainier National Park, Washington, I came upon a series of specimens (*Camp 104a, 104b, 105, 106a, 106b*) which seemed to further link these two species (figure 1).

Recently, in reviewing these sheets in conjunction with the material available in the Herbarium of the New York Botanical Garden I noticed, for the first time, a curious coincidence: a series of paired (or nearly

certain of these forms, such as the rare non-green *Monotropsis odorata*, sporadic as it often is in its occurrence, may be completely parasitic on the fungus, this organism in turn being further associated with some chlorophyll-bearing ericaceous plant such as *Kalmia* or *Rhododendron*. For the spermatophytes of this type—and wherein the exact biological associations were not completely known—the late J. H. Schaffner used the term *phagophytes;* a term sufficiently inclusive to cover the ambiguity of these situations.—W. H. C.

paired) collections of both *P. aphylla* and *P. picta* from various parts of their common range. The specimens are as follows:

BRITISH COLUMBIA: Vancouver Island, Mt. Benson, July 13, 1908, *John Macoun 85606* (*picta*); *ibid. 85608* (*aphylla*).

CASCADE MOUNTAINS (no political division indicated): Barlow Road, July 24, 1894, *Francis E. Lloyd* (sheets not numbered).

WASHINGTON: *sin loc.*, in 1889, *G. R. Vasey 370* (*picta*); *ibid. 371* (*aphylla*). Mt. Rainier Natl. Park along Tahoma Cr., July 31, 1932, *Camp 104a, b; ibid. 105* (*picta*); *ibid. 106a, b*.

OREGON: near Prospect, Jackson Co., July 23, 1932, *Camp 57* (*picta*, in part); *ibid. 63* (*aphylla*).

IDAHO: near Rathdrum, Kootenai County, July 20, 1892. *Sandberg, MacDougall and Heller 674* (*aphylla*); *ibid. 678* (*picta*).

CALIFORNIA: Lake County, Foothills south of Mt. Sanhedrin, midway between Potter Valley and Hullville, July 14, 1902, *A. A. Heller 5860* (*aphylla,* isotype of f. *ramosa* H. Andr.); *ibid. 5861* (*picta*). Butte County, Chico meadows, elev. 4000 feet, July 23, 1914, *A. A. Heller* (sheets not numbered). Nevada County, Greenhorn Creek, Mt. Oro Dist., July 13, 1933, *F. A. MacFadden 10936* (*aphylla*); *ibid. 10939* (*picta*).

ARIZONA: Baker's Butte, *Dr. Edgar A. Mearns* (*picta*, intermediate forms and *aphylla*—these last on the same rhizome—on same sheet).

Was it chance alone that determined this pairing of specimens? If so, there is reason to suspect that paired collections of *P. picta* and *P. dentata* should also be on deposit, for, according to the literature, these species have at times been thought of as being merely phases of each other. But such was not the case. I found no evidence of pairs of collections between *P. picta* and *P. dentata* and only one example between *P. dentata* and *P. "aphylla."*

CALIFORNIA: Sierra National Forest, Madera County, Shuteye Mountain, elev. 6500 feet, August 19, 1907, *John Murdoch, Jr., 2535* (*"aphylla"*); *ibid. 2536* (*dentata*).

Explanation of Figures 1–4

Fig. 1. Series of specimens from Tahoma Creek, Mt. Rainier National Park, Washington, illustrating degrees of leaf reduction in *Pyrola picta* (except c, c').

c, c'. Two specimens now suspected of being nearly aphyllous forms of *P. chlorantha*. The typical form of this species was also present in the locality.

Fig. 2. *Pyrola picta.* Aphyllous and normal branches from the same rhizome, *Camp 57,* Prospect, Oregon.

Fig. 3. *Pyrola picta.* Typical leaf form, *C. F. Sonne,* Placer County, California, August 7, 1896.

Fig. 4. *Pyrola dentata.* Typical leaf form, *J. William Thompson 12453,* Josephine County, Oregon.

What, then, is the significance of this strong evidence of the pairing of specimens between *P. picta* and *P. aphylla*, the apparent rarity of it between *P. aphylla* and *P. dentata*, or the absence of it between *P. picta* and *P. dentata?* Several avenues are open to our hypotheses. It is quite possible that both *P. aphylla* and *P. picta* have the same, or nearly the same, habitat requirements, whereas *P. dentata* has a different set. The rarity of closely paired collections of *P. dentata* with either of the other two would seem to lead to this conclusion.

So far as the status of *P. dentata* is concerned, I now feel that it should be recognized as a valid species, separate from *P. picta*. This conclusion is certainly not based on its altitudinal distribution, covering as it does the range of *P. picta* by occurring from the Humid Transition Zone into the Canadian Zone (there sometimes assuming the form called *P. dentata* var. *integra*) but, rather, on other characters, particularly those of the leaves. In general, the leaf-veins of *P. picta* are broadly white-margined, while those of *P. dentata* are not. But this character is, I think, of only minor importance in our fundamental interpretation of these species. In *Pyrola*, the pattern of leaf-shape is of greater significance. I am unable to associate, in any subspecific category, *P. dentata* with its strong tendency toward a spatulate leaf form with *P. picta*, whose leaf blades have a much stronger tendency toward ovateness, with a rounded base (figures 3, 4). Simulative intergrades between the two seem not to be more than casually common. Conversely, on the 40-odd sheets immediately available, I find ample evidence of a close and continuous series of intergrades between *P. dentata* and its so-called variety *integra*. These intergrades, sometimes on the same sheet or even on branches from the same rhizome, form so close a series that I am unable to follow Piper (l. c.) who, in his key, separates these two (there treated as varieties of *P. picta*) by their leaf shape and glaucescence. In any event, the reduced and shortened leaf blades on occasional specimens from high altitudes or dry sites follow the pattern of *P. dentata* much more closely than they do that of *P. picta*, so much so that I cannot assign to them even varietal rank under *P. dentata* without additional evidence to the contrary. Neither do I feel that the systematic scheme proposed by Andres would do more than add to our perplexity.

We now approach the problem of *P. aphylla* and *P. picta*. It has been said that a species consists of "a type specimen and its description." This could, with equal implication, be said of varieties and, although the foregoing quotation was made in jest, it becomes pointedly true if we attempt any rigid interpretation of such described entities as *Pyrola aphylla* var. *paucifolia* Howell [= (?) *Pirola aphylla* var. *foliosa* H. Andr.]; *Pirola picta*, subsp. *P. picta*, var. *sparsifolia* H. Andr. [= *Pyrola sparsifolia*

Suksd.]; or *Pirola picta*, subsp. *P. picta* var. *Suksdorfii* H. Andr. Andres was fortunate in knowing these only from single collections for, when we bring a series of such things together, we note that no two of them have the same leaf size. As a consequence, no line can, in either case, reasonably be drawn between the species proper, their so-called varieties, or their extremes.

Andres, probably following somewhat the lead of Piper (l. c.), apparently solved the basic problems of distinction between *P. aphylla* and *P. picta* on the basis of differences in inflorescence color and, in addition, flower size. If one now examines the previously cited pairs of specimens one is struck by the strong similarity (even in the dried plants) of the members of the pairs in both characters.

Looking further at additional specimens, one is unable to see any constant differences in flower size or structure that might be used to differentiate these two.

Also, a random sampling of 25 specimens each of both species was made to determine the average number of flowers per inflorescence. The results were as follows:

> Extremes: *P. aphylla*, 5–29; *P. picta*, 6–24.
> Average: *P. aphylla*, 14.5; *P. picta*, 12.5.

Although the averages may be statistically significant, it is obvious from the extremes that the number of flowers per inflorescence is of no use as a key character.

So far as color is concerned, little can be ascertained with positiveness from dried material, but specimens of authentic *P. picta* are available wherein definite evidence of a "purplish" or "pinkish" color remains, sometimes equal to the average color of *P. aphylla*. Further evidence of the inconstancy of inflorescence color as a clear-cut diagnostic character differentiating *P. aphylla* from *P. picta* may be obtained from St. John (1937), who clearly states (pp. 307, 308) that *P. aphylla* may be red or pink and *P. picta*, purplish tinged. Jepson (1925, p. 737) also states that the corolla of *P. picta* is "greenish-white or brownish flesh-color," and that of *P. aphylla* is "whitish or flesh-colored." In general, however, it would seem that the inflorescence structures of *P. aphylla* tend to be more deeply tinged with pink or red than those of *P. picta*. The "brownish" colors recorded by Jepson and also by Rydberg (l. c.) are, according to my own field observations, probably due to a combination of pale chlorophyll green, a pink or red pigment, and also, possibly, certain flavones likely to be present in the structures.

How, then, may we distinguish between *P. aphylla* and *P. picta?* If the color of the plant, the number of flowers, and their size are no sure criteria, can we rely on the presence of basal leaves? Andres (l. c.) was not cer-

tain of this matter, otherwise, under the normally broad-leafed *P. picta*, he would neither have recognized var. *sparsifolia* (Suksd.) H. Andr., nor described var. *Suksdorfii* H. Andr., this last *a completely leafless form*. The further apparent intergrades between both "species" in my collections from Mt. Rainier National Park and that curious specimen from near Prospect, Oregon, with both on the same rhizome, in conjunction with the previously cited paired specimens, certainly do not quiet the conscience of the taxonomist who would like to keep them separate.

There is, obviously, no great series of these intermediates between *P. aphylla* and *P. picta* in herbaria. This, I think, may in part be accounted for by the fundamental psychology of the average collector. It is only reasonable, and commendable, that the collector take a certain pride in the appearance of the specimens which he places on deposit. Also, in many instances, he is making a representative collection of the "species" from within his local area and pays but little attention to what to him appear to be the merely stunted individuals; rather, he collects what he has always considered the normal form. To be sure, he assiduously collects the bizarre and sometimes pathologic individuals—all too often forgetting to take the normal forms which grow beside these monstrosities, or to record the fact of their proximity—but he hesitates to collect those plants which he thinks will not bring credit to his reputation as a collector of "good specimens." Those plants with chlorotic and poorly developed leaves (to him only malformed individuals of *P. picta*) are passed by in favor of the more obvious ones with their large leaves, beautifully mottled with a striking pattern of white and green. At the same time and sometimes nearby—still ignoring the intermediates—he will collect "that interesting, leafless, saprophytic plant, *P. aphylla*," thus increasing the list of species from his local area. In such a manner, the working taxonomist— dependent as he generally is on poorly annotated exsiccati, and through no conscious blunder, either on the part of the collector or himself—is often led into errors of interpretation.

However, lest I seem to be censuring the collector, it is to be admitted that either *P. aphylla* or *P. picta* may and in certain regions apparently does occur without the presence of the other. But, before we base any argument for the separateness of these two on any slight differences in their distributions, we must remember that almost nothing is known of their fungous associates or of the biology or geographic distribution of these host organisms. Herein may lie the eventual solution of our problem.

Holm (1898) has given what to him were conclusive arguments for the complete autophytism of *P. aphylla*. I feel, however, that the major premises upon which he based his arguments were faulty and that his conclusion was therefore unwarranted. Holm also states (l. c., p. 250) that

the roots of this species are "without any trace of fungal mycelia." This statement has been doubted by Henderson (1919, p. 57) who adds: "This seems rather improbable in view of the fact that all other members of the genus have been reported to have hyphae in the roots." It is also evident that Holm based his somewhat too conclusive argument on a single specimen, one branch of which bore a rosette of what he termed "proper leaves." In spite of what I think was a misinterpretation of the basic nutrition of *P. "aphylla,"* Holm did, however, make pertinent observations on the morphology and development of the plant; observations which need not be discussed here, and should not, until more work is done on a greater number of individuals, particularly in relation to similar structures in *P. picta*. From the standpoint of this discussion, the important contribution of Holm's work was to establish the previously supposed fact that the plant called *P. "aphylla"* could bear green leaves.

Therefore, on the basis of the foregoing data, a tentative conclusion may be reached concerning the relationship of *P. picta* and *P. aphylla*: that *P. picta* is a facultative parasite and *P. aphylla* its extreme variant. However, the preliminary nature of such a conclusion must be emphasized. It is certainly safe to assume that the roots of *P. picta* are normally in close association with the mycelium of some fungus and thereby receive a certain nutriment. But it is not necessary to maintain that the association is an obligatory one, involving but a single species of fungus. It is possible that with one species of fungus the plant develops large leaves, and with another a different set of physiological conditions are set up which ordinarily inhibits their full development. Also it is possible that, within a single species, minor variations in ecological conditions affect the fungus itself so that its basic physiological activities may differ, not only from place to place but even within the same general area. Neither dare we exclude the possibility of morphologically similar but physiologically different races within the same species of fungus, nor ignore any differential effects induced by "plus" or "minus" strains of the same species. One might go even further and raise the question whether the mononucleate (haploid) or binucleate (dicaryophytic) condition of the mycelium of the fungus, if either could be associated with the same plant, might not induce dissimilar reactions in the companion organism, resulting in the *P. "aphylla"* vs. *P. picta* form of differentiation.

The newer techniques for the isolation and culture of these mycorrhizal fungi might yield interesting results if applied to this particular problem. It is also suggested that the germination of seed and growth of the seedling on nutrient sterile media, much as is now done with the Orchidaceae, might furnish invaluable information towards a solution of the many problems surrounding these so-called species; problems not only of their nutrition

but also of their morphologic interrelations and consequent taxonomic interpretations. Are the differences between the "normal" forms of *P. picta* and *P. aphylla* genetic in nature, or are they due to differences in nutrition? Such questions are for the mycologist and physiologist rather than the taxonomist.

It is only reasonable to assume that, in the group of *Pyrola* species here under discussion, a considerable portion of their basic food materials is almost certainly derived from their fungous associates. This is certainly true of *P. "aphylla"* wherein host-parasite relations would seem to be completely developed. In *P. picta*, individuals are known with leaves so poorly developed that they appear to be non-functional, yet the aerial structures seem to be as well developed as those with large leaves.

This lack of correlation between the leaf size and vigor of·the inflorescence in *Pyrola picta* is in rather sharp contrast to the condition in, for example, *P. uliginosa* and such other species as *P. americana* and *P. asarifolia*, or even their near relatives, *Erxlebenia minor* and *Ramischia secunda*, in which there is a strong correlation: the reduced inflorescences with their fewer and smaller flowers generally appearing on plants with reduced leaves. In none of these last, however, have I ever seen the leaves reduced to the extent they are in *P. picta*. Rather, the whole plant has the appearance of being depauperate.

If the reduction or even loss of the leaves of *P. picta* does not result in a correlative reduction in the inflorescence, it seems only proper to assume that the sparse chlorenchyma of its white-mottled leaves functions either poorly, or not at all, so that these structures are actually a drain on the food reserves of the plant rather than nutritive, photosynthetic organs. In this connection it should be recalled that the inflorescences of *P. aphylla* appear to average somewhat larger than those of *P. picta*.

The variability of the red pigment (water-soluble, and therefore probably an anthocyan of some sort) in both *P. aphylla* and *P. picta* has been mentioned. Also, the rôle of excess food supplies in the synthesis of these pigments is too well known to merit discussion at this point. It would seem that we might explain the apparently deeper red color of *P. aphylla* over that of *P. picta* on the basis that this leafless parasite generally has more food material available than the leafy *P.·picta;* that the latter dissipates its food reserves in the maintenance of a display of poorly functional leaves wherein respiration slightly exceeds photosynthesis. I make no apology for these hypothetical speculations. They are only the questions which must be answered before we can, with surety, arrive at a definite conclusion concerning the relative taxonomic position of these forms.

For the present, I think it should be recognized that a set of intergrades does exist between typical *P. picta* and derived leafless forms; a reduction

of leaf area resulting ultimately in plants which I, at least, am unable to separate adequately from what has been considered as typical *P. aphylla.*

In his monographic study, Andres (l. c.) states that leafless forms of his *P. picta* subsp. *pallida* (Green) [= (ex Andres) *P. picta* Sm. var. *integra* (Gray) Piper] have been noted, but omits mention of them under his subsp. *dentata.* As outlined previously, I am unable to separate these two forms. Andres cited no examples under this note, nor am I able to select with certainty any particular ones from the material now labeled "*aphylla*" that might belong here. There is, of course, the previously cited *Murdoch 2535* from Shuteye Mountain, Madera Co., Calif, which, except for its lack of foliage leaves is, in most respects, very similar to *Murdoch 2536* (*P. dentata*). It is suggested, however, that certain of the observed forms of *P. "aphylla"* with glaucous, basal leaf-bracts may represent possible aphyllous forms of *P. dentata.* Field study will be necessary either to substantiate or disprove this viewpoint.[2]

A species that has seldom been associated with this group is *P. chlorantha* Sw. What its intra-generic phyletic relationships with the previously discussed species may be I am not as yet prepared to say. Biologically, however, there are certain marked similarities for, as Fernald (1920) remarked: "In the White Mountains and across the northern half of Maine . . . . *P. chlorantha* is often quite leafless or has only a few leaves. . . ." Even though these leafless forms are only parenthetically mentioned in the key, the part of his Latin description of var. *paucifolia* dealing with these organs is certainly clear: "foliis nullis vel paucis. . . ." Judging by this character alone, I find that specimens of this species with reduced leaves, or even aphyllous—the leaves reduced to mere bracts,— are relatively common, not only from Michigan eastward, as the specimens cited by Fernald would seem to indicate, but also throughout the western parts of the species' range in North America. The floral characters given by Fernald seem neither striking nor constant enough to be of great service in delimiting his variety from the more typical form of the species as it is found in its broader distribution across America. It seems rather that *P. chlorantha* is only an additional species of this genus which, with its other variabilities, quite regularly and throughout its range, at least in America, has aphyllous forms.

These aphyllous forms of *P. chlorantha* may be separated from the similar forms of *P. picta* (or *P. aphylla*) by the same floral characters that distinguish the species. Among these may be mentioned particularly the relatively shorter and more obtuse (or even rounded) calyx lobes of

[2] Since this was written, a series of specimens has been received from Mt. Shasta, California, which would seem to further substantiate this suggestion; they include aphyllous forms more nearly matching the *P. dentata* specimens than those of *P. picta,* all three forms having been collected from nearly adjacent areas along the same trail.

P. picta (and *P. "aphylla"*). It is on this basis that I have separated aphyllous material seen in Mt. Rainier National Park (fig. 1, *c*, *c'*) and on the Olympic Peninsula, Washington, from *P. "aphylla."* Typical *P. chlorantha* was present in the immediate locality in both instances.

NOMENCLATURAL CHANGES

On the basis of the material here presented, the following nomenclatural changes are proposed:

Pyrola chlorantha forma **paucifolia** (Fernald) Camp, stat. nov.

Pyrola chlorantha var. *paucifolia* Fernald, Rhodora **22**: 51. 1920.

Pyrola picta forma **aphylla** (Smith) Camp, stat. nov.

Pyrola aphylla Smith, in Rees, Cycl. **29**: *Pyrola* no. 7. 1814.

Pirola picta, subsp. *P. picta,* var. *Suksdorfii* H. Andr. Allg. Bot. Zeitschr. **20**: 113. 1914.

It is to be admitted that, as here interpreted, these forms are not of exactly equal rank for, in his original description of *P. paucifolia*, Fernald included both reduced-leaved and aphyllous forms; whereas *P. aphylla* Smith applies only to the aphyllous form. No great confusion is envisioned if this usage is adopted for, after all, it would seem to more closely represent the biological actualities of the situation: the extreme aphyllous condition of *P. chlorantha* appearing to be relatively rare, whereas *P. picta* forma *aphylla* is much more common and, therefore, should be defined with more exactness.

The descriptions of these species should also be emended so as to clearly indicate that all gradations of intermediates are to be expected between the leafy and aphyllous forms. The formal recognition of the various degrees of intergradation would, I think, place an unnecessary burden on the literature of this group and certainly would not lead to a better understanding of its interrelationships.

SUMMARY

The genus *Pyrola* is on the borderline between autophytism and parasitism, forms of certain species apparently being quite able to flower and produce seed without functional leaves. It is suggested that these forms are, to a large extent, parasitic on the mycorrhizal fungi associated with them.

Species wherein aphyllous forms are known to be fairly common throughout their ranges are *P. chlorantha* Sw., and *P. picta* Sm., with *P. dentata* Sm. (here maintained as separate from *picta*) also suspected of having them.

It is suggested that *P. picta* Sm. is closest to the parasitic condition and that the well-known *P. aphylla* Sm. is only the extreme condition of this species.

The ultimate solution of the various problems here outlined does not lie in herbarium study but,. rather, in more careful field work coupled, it is to be hoped, with aid from the geneticist, the physiologist, and mycologist. I commend this problem of aphylly in *Pyrola*, particularly that of the *aphylla-picta-dentata* complex, to my co-workers in western North America who, being closer to it in the field, can hope eventually to solve it.

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Second-division Segregation and Crossing-over in the Fungi [1]

B. O. DODGE

(WITH TWO FIGURES)

Fifteen years ago it would have been a comparatively simple matter to prepare a résumé of all that was known regarding Mendelian inheritance in the fungi. Up to that time genetic work with fungi was mostly confined to the study of segregation of the factors determining sex reactions. Burgeff (1914, 1915) obtained a number of mutant races and designated them by genetic symbols. He mated these mutants and proved that the factors for sex and for different types of growth segregate according to Mendelian principles. To him must go the credit for first interpreting genetically cultural work with fungi, although Blakeslee's (1904) proof of heterothallism provided the real basis for much of this work.

I was privileged recently to hear a very scholarly review by Professor Alexander Weinstein of the Lindegrens' (1937, 1939) evidence supporting a theory of non-random crossing-over. Stated in simple language by this speaker, non-random crossing-over means that a crossing-over at one level between two non-sister chromatids at a four-strand stage affects crossing-over between the same two chromatids at other levels.

In genetic studies of animals and seed plants an analysis of all four progeny derived from the reduction divisions of a single mother cell is impossible because three of the four are lost as polar bodies, or by degeneration (in the ovule of seed plants). Geneticists are now looking with favor upon any organism which is well adapted for study of all four of the gametes (progeny). While in certain groups such as the higher basidiomycetes, the smuts, and certain species of liverworts it is possible to analyze all four haploid progeny of one cell, such ascomycetes as the 8-spored species of *Neurospora* are even more favorable for studies of crossing-over, because the spindles are so oriented at the first, second, and third divisions in the ascus that one knows the exact relationship of the eight nuclei (Dodge 1927, 1930; Wilcox 1928). Alternation in an ascus of pairs of spores bearing different factors indicates a second-division segregation of those factors.

Kniep (1922) for the first time isolated the four spores from individual basidia and suggested that the sex reaction of certain species must be governed by two independent pairs of factors *Aa*, *Bb*. Later his students

and colleagues and those of Buller investigated a number of species of mushrooms to determine whether their sexuality was "bipolar," *AB, AB, ab, ab* (*Ab, Ab, aB, aB*), with two kinds of spores, or "tetrapolar," *AB, ab, Ab, aB*, with four kinds of spores. In the end these workers all found that in certain heterothallic species some basidia are bipolar while other basidia in the same fruiting body are tetrapolar. From those early days to the
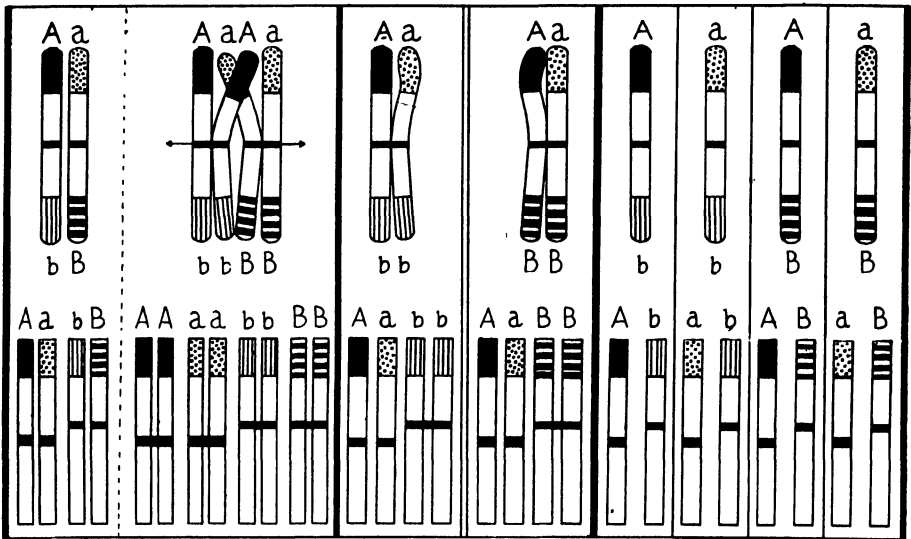
Fig. 1. Above: one pair of chromosomes. Diagrams showing how four kinds of nuclei can result from crossing-over where two pairs of linked genes are involved. The parental gametes in the mating are *Ab, aB*. The centromeres, indicated by the heavy black lines across the center in each case, must always reduce in the first division. Below: two pairs of chromosomes. Diagrams showing how Newton and others would account for the formation of four kinds of nuclei and therefore four kinds of spores in a basidium, according to the theory that the reduction of one pair of chromosomes, in this case *Bb*, can occur in the first division while the second pair, in this case *aA*, can reduce in the second division. Random distribution thus would operate to provide four kinds of spores. It will be shown that this sort of explanation is no longer acceptable.

present practically all who have studied smuts and higher basidiomycetes genetically have explained tetrapolar basidia as the result of segregation of one of the two pairs of factors at the first division and the other pair at the second division in the basidium. Until Newton (1926) gave us diagrams of chromosome behavior during the two nuclear divisions no one had attempted to explain the mechanism of such types of segregation in the fungi. Her scheme was adapted in part by Kniep (1929), the essential idea being that one pair of chromosomes could reduce in the first division while the second pair could reduce at the second division (see figure 1, below).

Lindegren (1936, 1939) has now[2] very good proof that normally the reduction of the centromeres occurs only at the first division of meiosis. Accordingly one can no longer explain tetrapolar basidia or asci with four kinds of spores as the result of the reduction of one pair of chromosomes in the first division and another pair in the second. *By means of a simple cross-over, segregation of factors can occur in the second division though the chromosomes disjoin in the first division.* In the light of this new viewpoint regarding the fungi it may be worth while to examine briefly some of the data furnished by certain students of the basidiomycetes to see if they have given us evidence either for genetic linkage or for crossing-over.

Newton's (1926) very ingenious and elaborate explanation to account for her 25 tetrapolar basidia now becomes a very simple matter. Of 42 basidia (zygotes) 25 formed four kinds of spores, *AB*, *Ab*, *ab*, *aB*, after reduction. Nine basidia produced only two kinds, *AB*, *AB*, *ab*, and *ab*, while eight other basidia also formed only two kinds, *Ab*, *Ab*, *aB*, and *aB*. Newton says that her data fit perfectly her assumption, which is made clear in her conclusion: ". . . . it seems impossible to explain the experimental data unless one accepts the view that disjunction of homologous chromosomes may take place either at the first or at the second of the two divisions of the fusion nucleus." While the genotypes of the parental gametes in her matings are not known, we may assume that the matings were either *AB* × *ab* or *Ab* × *aB*, because her two types of bipolar basidia are practically equal in number. A simple cross-over in each basidium accounts perfectly for the 25 tetrapolar basidia. Reduction in the first division and random assortment without genetic linkage account for both kinds of bipolar types.

Brunswick's (1926) results can be accounted for in exactly the same way. Again one has to guess at the genotypes of the parent gametes. His basidia probably all resulted from the same mating, however. A simple cross-over in connection with each of his 37 tetrapolar types accounts for the four kinds of spores *AB*, *ab*, *aB*, and *Ab*. It will not be necessary to discuss a number of similar contributions that have come out since Newton's papers appeared. We may take up Dickinson's work; it is not such a simple matter to explain his results genetically according to Lindegren's theory of second division segregation as determined by crossing-over.

[2] At the time when he first described crossing-over in *Neurospora* (1933) he had only two linked genes, *pale* and *sex*, at his disposal, too few to furnish a satisfactory basis for his argument. Now with five or six linked genes at his command he can prove that second division segregations, with certain corrections, are measures of crossing-over percentages. This view should be accepted as axiomatic now that in other organisms large numbers of genes have been located on the same chromosomes. With disjunction in the second division the number of combinations possible without crossing-over would be strictly limited by the number of chromosomes (and mutations and other intrachromosomal aberrations).

Dickinson (1931) assumed that in the oat smut *Ustilago Kolleri* first division segregations could be distinguished from second division segregations by isolating the sporidia in order from each of the four cells of the promycelium and growing them in culture. This is the same idea as that previously put forward by the writer and by Wilcox for *Neurospora sitophila*. The cytological evidence supporting this assumption is more convincing for *Neurospora*. Dickinson worked with seven (as he says) independently segregating characters and concluded that his results furnished further evidence for the theory that one chromosome pair may reduce in the first division while another pair may reduce in a second division. Lindegren (1933) failed to mention this important contribution, which represents several years' work on the genetics of this smut. Dickinson's color characters, brown, cream, and yellow, are determined by two pairs of factors *Aa, Bb*, which are additive in their effects, *AB* causing brown color, *ab* causing cream, and either *Ab* or *aB* causing yellow color.

Dickinson's six segregation schemes (1931, p. 419) are shown below with certain minor changes. These schemes were based on data given in his Table IX (p. 412, top). He assumes, as have many others, that it is the genotype of the zygote that is the all-important feature. By a careful reading of his text and his preceding papers, one can determine the genotypes of the two gametes which he mated. The haploid parental mating was *AB* × *ab*, that is, brown × cream.

Scheme I.   AaBb
$$AABB \qquad aabb$$
$$AB \quad AB \quad ab \quad ab$$
(No. found: 8)

Scheme II.   AaBb
$$AaBb \qquad AaBb$$
$$AB \quad ab \quad AB \quad ab$$
(No. found: 15)

Scheme III. AaBb
$$AAbb \qquad aaBB$$
$$Ab \quad Ab \quad aB \quad aB$$
No. found: 0?)

Scheme IV. AaBb
$$AaBb \qquad AaBb$$
$$Ab \quad aB \quad aB \quad Ab$$
(No. found: 4?)

Scheme V.   AaBb
$$AaBb \qquad AaBb$$
$$AB \quad ab \quad Ab \quad aB$$
(No. found: 8)

Scheme VI. AaBb
$$AABb \qquad aaBb$$
$$AB \quad Ab \quad aB \quad ab$$
(No. found: 0)
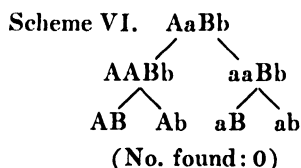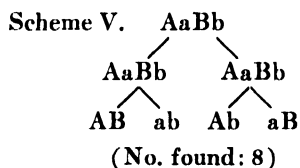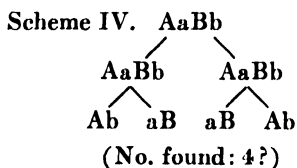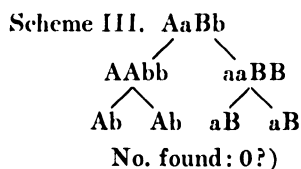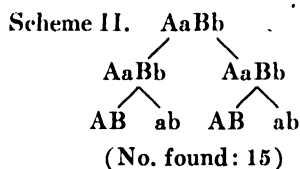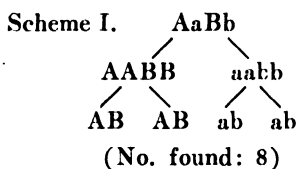
In all 35 zygotes are represented here. Disregard for the present the actual location of the sporidia on the promycelia, merely considering the number of old combinations as against the new combinations represented in the 140 haploid f_1 offspring sporidia. We find that 32 (22.8%) represent new combinations and 108 (77.2%) old combinations, which is proof of a real genetic linkage. The "additive linkage" postulated by Dickinson when he says: "In addition the sixth scheme in which the pairs of factors are segregated in different nuclear divisions should be found unless the two pairs are connected or show linkage" is phenotypic. It is apparently a

linkage of effects rather than of factors, for he says (p. 419): "The proportions given in Table X indicate that colour factors are segregated about 2½ times more frequently together than separately." Now in this table the heading is: "Ratio of divisions where brown and cream resulted to those where yellow resulted." Dickinson's segregations here are pheno-typic rather than genotypic. If he had mated two "yellows" together he
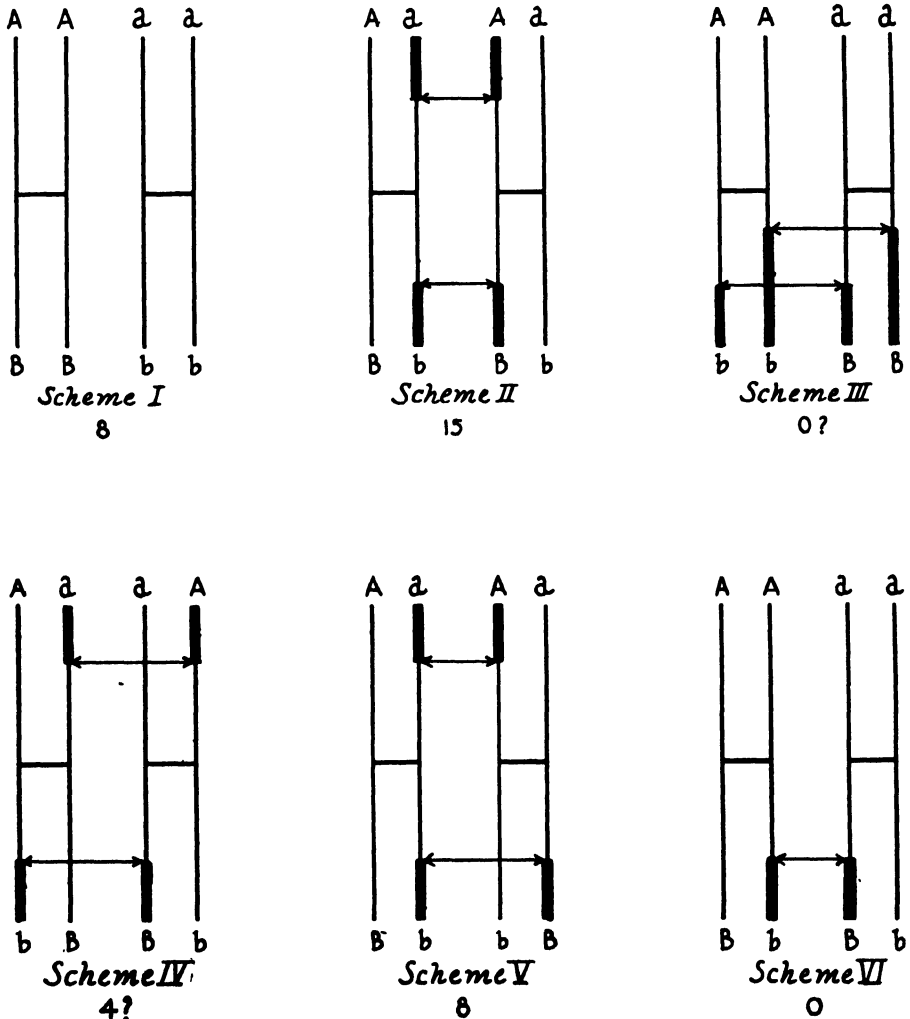
Fig. 2. Diagrams of types of crossing-over to illustrate Dickinson's Schemes I–VI, but on the theory that the centromeres (indicated by cross lines connecting the two daughter chromatids) reduce in the first division. The location of the genes is purely arbitrary, as are the lengths of fragments which have exchanged in the cross-over. Of the five possible types of crossing-over Scheme VI should occur the most frequently and Scheme III the least frequently.

should have found in the next generation that the color factors segregated *together* only two-fifths as frequently as *separately*. True linkage, *A* and *B* on one chromosome and *a* and *b* on the homologous chromosome, would not explain the lack of any segregation type like that shown in his Scheme VI. The wonder is that he did not find more of this than of any other type, for Scheme VI calls for merely a simple cross-over, while Scheme II, represented by 15 zygotes (promycelia), calls for a double cross-over in each case. Schemes IV and V also demand complicated series of cross-overs, as shown in the diagrams below. To prove that reduction of the centromeres always occurs in the first division, Lindegren (1933) used much the same line of reasoning and analysis as that presented by Dickinson, who did not consider crossing-over as an explanation of second-division segregation, but, rather, assumed that reduction (disjunction) of a pair of chromosomes may occur in either of the two divisions. To explain Dickinson's data, following Lindegren's (1933) line of analysis, results in some striking numerical oddities when it comes to percentages of certain types of crossing-over.

Furthermore, if one computes map distances, following Lindegren's outline but using Dickinson's figures, factors *A* and *B* would be 22.8 units apart on the basis of new-combination percentages, but on the basis of second-division percentages they would be either at the same locus or 77.2 units apart. One simply cannot reconcile the two different viewpoints of Lindegren and Dickinson. Lindegren (1936, 1937) has now adequate proof, because of the discovery of five or six linked genes, that the centromeres always reduce in the first division, and second-division segregations are explained as due to crossing-over and not to reduction (disjunction) of chromosomes in the second division. It would, therefore, be very simple to assume that the positions of the sporidia on the promycelia of *Ustilago Kolleri* are not an altogether reliable basis for distinguishing first- from second-division segregation. In that case Dickinson's Scheme II would be ruled out, the 15 zygotes going to Scheme I. Scheme IV could still remain, as the type of crossing-over in Scheme III, two independent simultaneous cross-overs at different levels, is rare. Scheme V would fall out, the eight promycelia going to Scheme VI, where a simple cross-over would account for the four types of sporidia.

Ustilago Kolleri (*U. levis*) is widely distributed and wild races with the same genes as those used by Dickinson must be available. It would be interesting to carry on matings through the F_2 generation and mate two yellow races. If the color characters are determined as Dickinson suggested, and not like *tan* in Lindegren's *Neurospora*, and if the cross-over percentages hold, one should obtain on the same basis 108 yellow races to 16 brown and 16 cream colored races out of each 140. When he mated

brown and cream races the numbers were 54 brown, 54 cream, 32 yellow. Since the factors for sex and the factors for color are not linked one could mate certain yellow races and no cream or brown should appear in the progeny. Thus the genotype of any yellow race can be determined by mating it with a standard tester race of the opposite sex, the symbol of the tester being fixed at the start as either Ab or aB. Dickinson was forced to assign these symbols to all his yellow races arbitrarily in his schemes III to VI.

The four spores formed after reduction in the mother cell of the liverwort *Sphaerocarpos* adhere in tetrads, so that Allen (1925–1930) could grow the four progeny separately and inbreed haploid individuals originating from the same zygotes. Because of the very small size of the Y-chromosome he doubts that there can ever be a cross-over involving the X and Y chromosomes. Furthermore, he doubts that maleness and femaleness can be represented by pairs of genetic factors or factor complexes that are inherited as units in Mendelian segregations; that is, that $♀/♂$ can be represented by $+/—$ or A/a symbols. He also rejects the thought that P/p are located on the X/Y chromosomes. He does admit the possibility of a crossing-over involving P and p to account for second division segregation and tetrapolar tetrads, because P/p are not on the X, Y chromosomes.

From Allen's Table 7 (1930) we gather that from the parental matings $♀p \times ♂P$ he was able to analyze the progeny of 70 tetrads. He has grouped his results in three classes as follows:

Class (1) 39 (56%) tetrads were $♀p$, $♀p$, $♂P$, $♂P$ parental combinations
Class (2) 19 (27%) tetrads were $♀P$, $♀P$, $♂p$, $♂p$ new combinations
Class (3) 12 (17%) tetrads were $♂p$, $♀P$, $♀p$, $♂P$ two new and two old combinations

In Allen's summary (1935) he says, "The preponderance of Class (1) over Class (2) indicates something like a linkage between sex and the polycladous character, but since a crossing over between the X and Y seems out of the question, it has been suggested that there is in this case a tendency for certain chromosomes derived from each parent to pass to the same daughter nucleus in meiosis." This would be a new kind of linkage which, if true for *Sphaerocarpos*, could be true for *Drosophila* and maize. The percentage of new combinations listed by Allen (35.6) should indicate a real linkage, but Allen's Class (2), 19 tetrads, would then have to be explained as due to two simultaneous independent cross-overs—altogether too many to expect when single cross-overs occurred only twelve times. One can, therefore, best explain Allen's results by supposing that there is no linkage between the sex and polycladous factors and that the reduction occurs in the first division. A simple crossing-over or exchange of p and P in the twelve tetrads in Class (3) would give the four kinds of

spores. Classes (1) and (2) would probably become more nearly equal with analysis of a greater number of zygotes.

Unfortunately, Allen cannot carry on matings into the second generation to test for linkage and crossing-over because the new combination ♀ *P*, female polycladous, is invariably sterile; which in itself is interesting if there are no genetic linkages involved. In another connection, Allen (1925) finds a strongly sex-linked character or factor which determines whether the four spores of a tetrad are united or separate. This is a diploid or sporophyte character and the factor, located on the X chromosome, determines the inheritance, united or separate spores. Allen has carried this through a number of generations, finding only one case indicating that the factor for separate spores had crossed over to the Y chromosome. His explanation of this on the basis of an error in records or contamination of culture, however, seems to stand, for the writer finds no later mention in Allen's papers of matings proving that the Y chromosome involved did actually carry the factor over to any subsequent progeny. He assumes that the original appearance of this factor resulted from a mutation.

The writer has not found in Burgeff's (1928) painstaking analyses of his cultural results with *Phycomyces* any statement to the effect that he believed he was ever dealing either with true linkages or crossing-over. He concluded that when four types of progeny developed from the germination of a zygospore, this was due to reduction of one of two pairs of homologous chromosomes at the second division.

Sansome and Philp (1939) discuss briefly genetic work on the fungi, beginning with that of Burgeff. They give us (p. 52) the old familiar formula diagram showing how, by the segregation of one pair of factors in the first division and another pair in the second division during meiosis, four kinds of spores or races can be obtained. Such diagrams tell us nothing of the mechanism involved. Their legends *c* and *b*, explaining the diagrams, are transposed, which is very confusing. Some of the earlier work on the fungi is noted, but they do not point out any concrete examples of what they consider proof of either real genetic linkages or crossing-over. They do, however, give a brief review of some of the work on *Neurospora* in which crossing-over was mentioned.

It is difficult to analyze genetically some of the results that have been recorded by mycologists working on the genetics of fungi, because, as noted previously, the authors have not always appreciated the importance of determining or stating the genotypes of the parental gametes. Allison (1937) presents a very interesting diagram and says that it shows Mendelian segregation of factors for sex, dominance of rough over smooth, and recombination. That there must have been recombination is clear, but since he does not give the full genotype of either parent and does not

analyze the progeny of the F_2 chlamydospores, one cannot tell whether in the parental gametes the S was + and the s was — or vice versa.

Lindegren has emphasized the importance of inbreeding these fungi to obtain pure lines with which to begin work. Unless the future proves the contrary, breeding results must be analyzed on the basis that in the fungi as elsewhere reduction of the centromeres always occurs normally at the first division. Second division segregation, therefore, must be attributed to crossing-over. Both Allen and Lindegren have expressed the importance of stating the genotypes of the gametes mated. This is an important factor in determining the presence or absence of linkages on the basis of recombination percentages. With due consideration for these principles, breeding work on the fungi is bound to take on greater significance.

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Late Tertiary Floras of the Great Basin and Border Areas

Daniel I. Axelrod

INTRODUCTION

In addition to pointing out the general features of the northern Tertiary redwood flora, Asa Gray indicated also that a large part of the modern flora in the western United States may have had an origin in northern Mexico (1859; 1878; 1883). Paleobotanical research has provided ample evidence in support of this concept of the twofold origin for much of the woody flora in western North America. The abundant fossil record of Washington, Oregon, Idaho, Colorado and northern California has made it possible to discuss the history of the northern redwood forest flora in considerable detail (Chaney 1936; 1938, see bibliography). On the other hand, the development of the north Mexican woodland flora has been outlined only in a general manner because fossil floras of woodland aspect have been unknown until but recently (Axelrod 1937, p. 144–145; 1938; 1939). A collection of 12 later Tertiary floras obtained from the Great Basin province during the past two summers is of considerable significance because these floras provide additional data relative to the composition and past distribution of the north Mexican woodland flora. In addition, they afford evidence about the general environment over the region and place rather accurately the southern boundary of the Miocene redwood flora in the Great Basin area. An analysis of the floras provides considerable evidence pertaining to the evolution of the woodland and montane forests into their respective modern communities and, finally, a study of the floras assists materially in formulating a paleobotanical basis for age determination. The floras of the Great Basin area, which are now being studied under the auspices of the National Research Council, were collected with funds made available by the Carnegie Institution of Washington. Because the work on these floras will not be completed for some time, it seems desirable to present a general statement of some of the major conclusions already reached about the later Tertiary vegetation and environment of the Great Basin and border areas.

Any interpretation of later Tertiary vegetation distributed over the area from southern Oregon and Idaho southward for 800 miles into the Mohave and Colorado Deserts, must be guided by an understanding of the middle Tertiary history of the region. It is therefore essential to distinguish between the floras which occupied the northern and southern parts of the province during Miocene time. The middle Tertiary redwood forest flora at the north is clearly of holarctic origin, and contains three distinctive elements, the redwood, broad-leaved deciduous, and Asiatic (Chaney

1936). The redwood element is made up of species whose nearest related modern descendants now form part of the redwood forest of California (Chaney 1925). In addition to the coast redwood (of the *Sequoia semper-virens* type), this group includes such plants as maple (*Acer*), alder (*Alnus*), dogwood (*Cornus*), tan oak (*Lithocarpus*), Oregon grape (*Mahonia*), and the California laurel (*Umbellularia*). Such an assemblage reflects a climate in which extremes of temperature were lacking, and in which rainfall was abundant. The broad-leaved deciduous group is represented by plants whose nearest modern equivalent species now occur in eastern North America. These species of hornbeam (*Carpinus*), hickory (*Carya*), beech (*Fagus*), sassafras (*Sassafras*), and elm (*Ulmus*), which were associated with the redwood element, suggest that rainfall was distributed rather evenly throughout the year in the northern Great Basin and Columbia Plateau during Miocene time. The Asiatic element is made up of species whose nearest modern correlatives now occur in eastern Asia, an area with a climate essentially similar to that of eastern North America. In addition to including some of the broad-leaved deciduous genera occurring also in eastern North America, this group also contains plants no longer indigenous to the continent, such as the katsura (*Cercidiphyllum*), maidenhair tree (*Ginkgo*), keteleeria (*Keteleeria*), and water-chestnut (*Trapa*).

The recorded distribution of this flora at many localities over the northern Great Basin and Columbia Plateau suggests widespread forests living under relatively uniform climatic and topographic conditions in areas where plants were accumulating. An annual rainfall of from 40 to 50 inches distributed rather evenly throughout the year, and moderate ranges of annual temperature, characterized the region. The occurrence of this Miocene type of flora and climate over the northern portion of the province, and its extension westward into the coastal regions, clearly indicates that the Cascade Range was sufficiently low at this time to have had relatively little effect as a climatic barrier (Berry 1929; Chaney 1938a).

In sharp contrast to this mesic forest flora is the arid north Mexican vegetation which occupied the southern portion of the province during Miocene time (Axelrod 1939). The dominant element includes species whose closest modern representatives now occur in southern California, the southwestern United States, and northern Mexico. Characteristic plants include Mexican madrones (*Arbutus*), buckbrush (*Ceanothus*), hackberry (*Celtis*), mountain mahogany (*Cercocarpus*), cypress (*Cupressus*), fan-palm (*Erythea*), desert barberry (*Mahonia*), pinyon pine (*Pinus*), cottonwood (*Populus*), mesquite (*Prosopis*), desert apricot (*Prunus*), xeric live oaks (*Quercus*), and evergreen sumach (*Rhus*). Distributed among such communities as desert scrub, chaparral, savanna, and oak-pinyon woodland,

this type of vegetation extended eastward from southeastern California and adjacent Nevada into northern Mexico. Conditions over the region were similar in many respects to the present southern Arizona climate. An annual rainfall of from 12 to 25 inches was distributed largely during two periods of maxima, as summer thundershowers and winter rains. Ranges of temperature were extreme, exceeding 105° F. in summer and reaching freezing in winter. The drier climate in this region, as compared with the northern Great Basin, is consistent with its location 700 miles farther south, where even today rainfall is lower and where higher temperatures give higher evaporation. It would appear that in Middle Miocene time the southern Sierra Nevada formed a more effective climatic barrier to the southern portion of the province than did the northern Sierra Nevada or Cascade Range to the northern Great Basin and Columbia Plateau.

LATE TERTIARY FLORAS OF THE GREAT BASIN PROVINCE

At the end of the Miocene and in early Pliocene time there was extensive uplift along the Cascade-Sierra Nevada mountain axis. The increased continentality over the Great Basin province at this time, which was due in large measure to the interception of rain-bearing winds by these rising mountain barriers at the west, reduced Pliocene rainfall from 10 to 12 inches below that of the Miocene. Instead of being distributed rather evenly throughout the year, rainfall at the north now appears to have been concentrated into the summer and winter months. Temperatures changed from moderate, with a low range of variation and few extremes of high or low, to higher ranges and greater extremes (Dorf 1936, p. 97). These latest Miocene and early Pliocene conditions were unfavorable for the widespread forests at the north. This is shown by the restricted nature of redwood, by the development of a border aspect to the redwood element, by the poor representation of the broad-leaved deciduous and Asiatic elements, and by the increasing numbers of arid southern plants. In other words, this climate was more nearly optimum for the arid north Mexican flora. Migrating northward, members of the southern element attained their greatest distribution in latest Miocene and early Pliocene time. They ranged northward through the Great Basin and into the Columbia Plateau, as well as westward into central California and eastward to Oklahoma (Axelrod 1939, p. 49–58).

The members of this arid north Mexican vegetation are represented in the three generalized communities which may be recognized over the Great Basin area during later Tertiary time. From north to south, these associations are: the relict redwood forest flora; a central oak-juniper woodland community; and desert-border vegetation at the south.

The *relict redfood forest*,[1] as judged from the later Tertiary floras of the province, ranged across the region of the present sagebrush lowlands of southern Oregon and Idaho, and extended southward along the Sierra Nevada and higher Basin Ranges into the central part of the province. Typical members of the montane forest include:

Abies	*Libocedrus*
Acer	*Lithocarpus*
Alnus	*Mahonia*
Amelanchier	*Pinus*
Arbutus	*Populus*
Betula	*Prunus*
Castanopsis	*Pseudotsuga*

Although the redwood is rare at the north and has not been recorded in central Nevada, members of the broad-leaved deciduous and Asiatic groups have a representation in this latter area. The relict occurrence of such regular northern Miocene genera as *Carya*, *Cebatha*, *Nelumbo*, *Trapa*, and *Zelkova* in the late Miocene at Coal Valley, near Wichman, Nevada (Axelrod 1940), indicates that the northern forest flora ranged southward at least to that area. As judged from their recorded absence in floras farther south, it would appear that the northern Miocene flora did not range over lowland areas south of latitude 38° in western Nevada during later Tertiary time.

Although members of the southern flora are associated with the montane community, a limited occurrence suggests that they occupied drier sites in the adjacent region. These include species of madrone (*Arbutus*), buckbrush (*Ceanothus*), mountain mahogany (*Cercocarpus*), silktassel bush (*Garrya*), juniper (*Juniperus*), barberry (*Mahonia*), pinyon pine (*Pinus*), oaks (*Quercus*), and locust (*Robinia*). Rainfall over the area of distribution of the relict redwood forest flora apparently varied from 20 to 30 inches, depending on location in the province, elevation, and position with respect to mountain barriers. Temperatures were considerably more moderate than those now obtaining over the area, and in general were like those now found along the western slopes of the Sierra Nevada.

The oak-juniper woodland community[2] characterized the central part of the province, with oaks and juniper dominant. The oaks, which may be compared with such modern species as *Quercus arizonica* Sargent, *Q. chrysolepis* Liebmann, *Q. Engelmannii* Greene, *Q. Douglasii* Hooker & Arnott,

[1] Members of the montane forest occur as an important element at Wieser, Idaho; Alvord Creek, Oregon; Fallon, Verdi, Chalk Hills, and Coal Valley, western Nevada.
[2] Members of the woodland community occur as an important group at Verdi, Fallon, Coal Valley, and Esmeralda, Nevada; Ricardo, Mint Canyon, and Mount Eden, California.

Q. hypoleuca Engelmann, and *Q. Wislizenii* DeCandolle, include the following among their regular associates:

Arbutus	*Garrya*
Arctostaphylos	*Juglans*
Ceanothus	*Mahonia*
Celtis	*Pinus*
Cercocarpus	*Populus*
Cupressus	*Rhus*
Diospyros	*Robinia*
Fraxinus	*Sapindus*
Fremontia	

Their wide distribution over the central part of the province suggests a rainfall of from 14 to 18 inches annually, and temperatures more nearly like those now found in southern California and southern Arizona. The limited representation of members of the northern forest in some of these woodland floras suggests that they occurred in the adjacent mountainous areas where rainfall was greater and temperatures more moderate.

It is significant that members of the Sagebrush formation, such as *Artemisia, Peraphyllum, Prunus* (aff. *P. Andersonii*), and *Purshia,* have been found associated with the woodland community. During later Tertiary time they probably occupied drier and more exposed sites over the region in a manner typical of their present occurrence in woodland areas.

The desert-border community[3] is composed of species whose closest living representatives are characteristic of arid regions throughout their ranges, and all are found bordering desert areas. They may grow on desert slopes and along desert washes, or may be present on deserts opposite the mouths of streams where moisture is more available than in the desert proper. Characteristic members of this group include the following:

Crossosoma	*Prosopis*
Ephedra	*Prunus*
Erythea	Palm cf. *Washingtonia*
Lepidospartum	*Yucca*

Although woodland species may have a representation in these floras, members of the montane forest are absent. Rainfall over the area of desert-border vegetation ranged from 10 to 14 inches yearly. In general, conditions now prevailing along the border of the Colorado and Sonoran Deserts most nearly approximate those of early Pliocene time in the southern Great Basin.

It is thus clear that 3 generalized communities occupied the Great Basin area during later Tertiary time. At the north, and extending south-

[3] Later Tertiary floras with desert-border vegetation occur at Ricardo, Mint Canyon, and Mount Eden in California, and near Wikieup, Arizona.

ward along the higher mountains, was a montane forest. A woodland community characterized the central part of the province and a desert-border flora occurred at the south. As judged from modern vegetation resembling these associations, rainfall ranged from 20 to 30 inches in the northern community, from 14 to 18 inches in the central woodland group, and from 10 to 14 inches in the southern desert-border association. In general, temperatures for the three communities resembled those now found along the western slopes of the Sierra Nevada, in southern California and southern Arizona, and along the borders of the desert in southeastern California and northern Mexico.

POST-LOWER-PLIOCENE FLORISTIC EVOLUTION

Post-Lower Pliocene climatic changes, resulting from the continued elevation of the Sierra Nevada-Cascade mountain barrier at the west, caused a further decrease in annual precipitation. The lowering of yearly rainfall over the province from early Pliocene to Recent is on the order of 10 inches, but varies from 5 to 15, depending on location with respect to mountain barriers and elevation. Effective summer thundershowers gradually ceased to occur in the province, and the ranges and extremes of temperature increased throughout later Cenozoic time. The floristic evolution in the woodland and montane groups which resulted from these climatic changes is summarized below.

With respect to the northern flora, the Asiatic and broad-leaved deciduous elements, as well as the climatically sensitive *Sequoia*, seem to have been eliminated from the province during Lower Pliocene time. Although a large part of the coniferous forest and its regular associates have survived to the present in modified form in the adjacent mountains, there have been important changes in distribution. These modifications, which were largely a restriction of range in response to changes in rainfall and temperature factors, have played a major rôle in the differentiation of four coniferous associations in western North America; the Redwood, Sierra-Cascade, Coast, and Petran (Clements 1920).

1. The redwood forest was limited coastward to areas of greater rainfall and moderate ranges of temperature (Chaney 1938a, p. 109; 1938).

2. The Sierra-Cascade association was segregated from the redwood forest and seems to represent an arid phase of that flora (Mason 1936, p. 188). Low winter temperatures appear to have been a critical factor in its elimination from the central and northern Great Basin, an area where members of the forest have a large later Tertiary representation.

3. The Coast forest was restricted northward and coastward to areas of greater rainfall.

4. Only the Rocky Mountain Petran forest has survived throughout the higher ranges over the Great Basin and adjacent areas. This is due probably to the wide ranges of tolerance of the component species.

Since the fossil representatives of these communities form a regular part of the Miocene forest flora, it is clear that the broad ecotone displayed by these four associations in northern California and southern Oregon has definite historical significance.

As for the woodland group (Clements 1920), there is ample evidence for the conclusion that this formation also was a generalized and undifferentiated community in later Tertiary time. The three modern associations, the oak-juniper of the southwestern United States and northern Mexico, the pinyon-juniper of the Great Basin and Colorado Plateau, and the digger pine forest of California, have been segregated from this community. Later Tertiary climatic changes relating to the development of the modern associations are as follows:

1. Regular dominants and typical associates of the oak-juniper association were restricted into the southwestern United States and northern Mexico as effective summer thundershowers disappeared from the western Great Basin.

   In areas of the northward extension of the community into the Rocky Mountain area, colder winter temperatures appear to have been an important factor in its southward restriction.

2. The digger pine forest of California was eliminated from central Nevada in response to low winter temperatures.

3. This same factor, extreme low winter temperatures, seems related to the southward retreat of pinyon pine from areas of its former occurrence in the northern Great Basin. The modern pinyon-juniper community of the Great Basin and Colorado Plateau is considered to represent a part of the north Mexican flora that became adapted to changing conditions at the north.

It is to be emphasized that the fields of plant physiology and paleobotany overlap when an attempt is made to explain the later floristic evolution of these woodland and montane floras. Although some of the major factors controlling distribution seem to be known, their rôle in plant distribution is not always clear. A fertile field for research would be a consideration of the factors controlling forest distribution, especially as related to the northern and southern boundaries of natural forest communities, and to their outpost occurrences.

In connection with the present areas of the pinyon-juniper woodland association in Nevada, it is significant that in some of these areas a dominant montane flora occurred in late Miocene and early Pliocene time. It

may be suggested that as rainfall was lowered, the montane forest was
restricted into the adjacent mountains where it now forms the Petran
forest, and that the pinyon-juniper association invaded the lowland areas
and has dominated regions of the former montane forest since Middle
Pliocene time.

Similarly, the Great Basin sagebrush now occupies much of the area
formerly inhabited by the late Tertiary woodland formation. Records of
the sagebrush formation have been found with the woodland group, and, as
has been already pointed out, these shrubs probably occurred as a seral
stage over the area in early Pliocene time. Perhaps moving northward with
the woodland group in the late Miocene, these plants gradually invaded
lowland areas as rainfall was lowered and the surviving pinyon-juniper
association was limited to higher elevations. In any event, the Great Basin
sagebrush is clearly post-Lower-Pliocene in its development as the climax
formation over the area.

CRITERIA FOR AGE DETERMINATION

The stratigraphic occurrence of fossil species in floras of known age
provides an index of age within a given region in Miocene or Eocene time
only because the forests of these epochs were relatively homogeneous and
widespread. The stratigraphic value of this method is weakened consider-
ably in later Tertiary time because the floral provinces are more narrowly
defined and a greater diversity of habitats is represented. Obviously, age
determination of later Tertiary floras from the standpoint of species pos-
sessed in common with floras of known age, even within a given province,
becomes largely a matter of correlating floras of similar ecological posi-
tion. Since the floras of the later Tertiary are highly localized in aspect and
vary widely in composition over short distances, comparisons must com-
monly be made between floras of different composition. In other words,
the problem of correlating these later floras is comparable to proving,
for example, that the modern redwood forest of coastal California is con-
temporaneous with the pinyon-juniper community of western Nevada.

As a basis for age determination of the later Tertiary floras in west-
ern North America, the north Mexican element is proving to be of greater
stratigraphic value than was at first expected (Axelrod 1938). This arid
southern element which migrated northward into the western United States
as the climate at the north became drier and warmer is now known to have
invaded each province only during a given stage, depending on latitude
and position with respect to mountain barriers and the ocean. Widespread
in the western Mohave area in early Middle Miocene time (Axelrod 1939),
the southern element appeared in the central part of the Great Basin
province during Upper Miocene, and invaded the northern Great Basin
and Columbia Plateau only at the end of that stage and in the earliest

Pliocene (Axelrod 1939, p. 53). The later appearance of the southern element in the area west of the Sierra Nevada and Transverse Ranges of southern California is explainable on the basis that humid conditions continued longer on the windward slopes of those ranges. The group occurs in southern California in Upper Miocene time (Axelrod 1940a), along the western slopes of the central Sierra Nevada during earliest Pliocene (Condit 1940), and in the San Francisco Bay area at the end of Lower Pliocene time (Axelrod 1940b).

It is to be emphasized that there is a direct relationship between the invasion of the arid north Mexican element into a province at the north, and the gradual reduction in numbers and elimination of the more mesic redwood, broad-leaved deciduous, and Asiatic elements of northern origin. The modification of these northern elements provides a further basis for age determination, because they show a rapid change in composition and distribution in later Tertiary time in response to the trend to aridity (Chaney 1936a). The representation of these elements differs in the respective provinces at any one stage in the later Tertiary. In Lower Pliocene time, for example, the broad-leaved deciduous element is abundant in west-central California (Axelrod 1940a), it forms a minor element in the

	GREAT BASIN & BORDER AREAS	SOME CALIFORNIA FLORAS
MIDDLE PLIOCENE	Mount Eden	Etchegoin
		Mulholland
	Alturas	
LOWER PLIOCENE	Truckee Ricardo Esmeralda Alvord Creek Idaho	Black Hawk Tuolumne Table Mt. Alamo
UPPER MIOCENE	Mint Canyon Coal Valley	Neroly

NOTE: The allocation of the floras to the major stages seems well established, but their chronologic arrangement is only approximate.

northern Great Basin, and is largely absent in western Nevada. The rela-
tive abundance of the northern elements in a province in later Tertiary
time is a reflection of the degree of aridity, and is proportional to the
development of the southern element.

Accordingly, only by recognizing a definite floristic sequence in each
province during the later Tertiary can a basis for age determination be
established which may prove to be significant stratigraphically. Also, only
by recognizing a definite floristic sequence in each province is it possible
to show that later Tertiary floras having few or no species in common may
be essentially contemporaneous. Fortunately, all the floras in the Great
Basin area with the exception of the Alvord Creek occur in association
with vertebrate faunas which have a known stratigraphic level. As now
understood, the relative ages of the floras in the Great Basin and border
areas are as shown in the table on page 485.

SUMMARY

An arid north Mexican flora ranged from northern Mexico into south-
eastern California during Middle Miocene time, when the redwood forest
flora lived in the northern Great Basin and Columbia Plateau. Late Mio-
cene and early Pliocene elevation of the Sierra Nevada-Cascade mountain
barrier along the western edge of the province resulted in a lowered rain-
fall and greater extremes of temperature at the north, allowing the north-
ward migration of many members of the southern element.

Later Tertiary floras distributed from southern Oregon and Idaho
southward for 800 miles into the Mohave and Colorado Deserts show
that the members of this north Mexican element are represented in the
three generalized communities which may be distinguished over the area
at this time: a relict redwood forest flora at the north, a central woodland
association, and a desert-border community at the south.

The nature of the climate over the region is discussed, later Tertiary
floristic changes are indicated, and a basis for correlation is presented.

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Experimental Phymatotrichum Root Rot of Retama and Corn [1]

G. M. WATKINS[2] AND MATILDE OTERO WATKINS

(WITH 27 FIGURES)

Several investigators have used very young seedlings growing under aseptic conditions in vitro as subjects for experimentally induced disease. The method has been employed in histological and cytological studies of watermelon (Butler 1935) and cotton (Watkins 1938a) infected with the fungus *Phymatotrichum omnivorum* (Shear) Duggar. The study of infected roots of cotton seedlings, as well as later work on naturally occurring *Phymatotrichum* root rot of field-grown cotton (Watkins 1938b), indicated that hyphal secretions play an important part in the attack and destruction of host tissues by the fungus.

Although all monocotyledonous plants and a number of dicotyledonous species are considered from field observations to be immune from *Phymatotrichum* root rot (Taubenhaus and Ezekiel 1936), the fungus has been observed by King and Loomis (1929) on roots of date palms and on root crowns of sorghum. The extent of parasitism in such cases is difficult to determine. Dr. C. H. Rogers (unpublished data), however, found damaging lesions produced by the fungus on roots of day lily (*Hemerocallis* sp.). In the work reported here preliminary experiments with several immune or resistant species, using the pure-culture technique referred to above, showed that all were attacked more or less readily in seedling stages by *P. omnivorum*. Two of these, retama (*Parkinsonia aculeata* L., Leguminosae) and corn (*Zea Mays* L.), were chosen for detailed observation, and from infected roots of their seedlings adequate material was preserved for cytological study. Both species are considered immune from the disease at maturity under field conditions (Taubenhaus and Ezekiel 1932, 1936).

MATERIALS AND METHODS

The procedure used in this work for preparing seedlings for inoculation was similar to that described elsewhere (Watkins 1938a; Watkins and

Watkins 1940). Seed of retama was collected from trees growing at Austin, Texas. After immersion for 4 hours in concentrated sulphuric acid, followed by washing and soaking overnight in water, almost all seeds germinated readily. The corn seed, obtained from commercial stock, was of the variety "Cream and Honey," a sweet corn. Seeds of both species were surface-sterilized by treatment with mercuric chloride solution, washed in sterile water, and placed on sterile potato-dextrose agar in Petri dishes. As soon as the majority of seeds in any given lot had produced seedlings with hypocotyls from 15 to 25 mm. long, all dishes were examined carefully for the presence of possible contaminating organisms. Contaminated plates were discarded; the remainder were inoculated by placing near the root of each seedling a block (approximating a 2 mm. cube) of sclerotia taken from a pure culture of *P. omnivorum*. The cultures were then incubated in an air-conditioned room at approximately 28° C. The process of infection in these plates was observed daily for a week or longer, and at times during this period, as the condition of the cultures suggested, variously infected seedling roots were removed and fixed in Allen's modified Bouin's solution. All material was embedded in paraffin in the usual manner and sectioned serially at 8–10μ. Three staining techniques were employed: the Flemming triple, the Heidenhain iron alum-haematoxylin, and the Pianeze IIIb.

OBSERVATIONS

In general the externally visible process of infection in seedlings of retama and corn resembled that described in detail for seedlings of cotton (Watkins 1938a). Hyphae growing out from the inoculum, which had been variously placed with reference to the seedlings, generally touched the roots in from 24 to 72 hours after inoculation, and then began to form characteristic delicate, white mycelial wefts which gradually spread over all parts of the roots. The enveloping hyphal sheath was at first a weft of sparsely distributed filaments which interlaced with the root hairs. Further

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Explanation of Figures 1–10

Figs. 1–10. Longitudinal sections of roots of retama seedlings inoculated with *P. omnivorum*. Fig. 1. Epidermis and outer cells of the cortex destroyed by substances absorbed from the sclerotial mass. The nucleus in the cell beneath appears more or less normal. Fig. 2. Similar to fig. 1, except the nucleus is dark-staining. Fig. 3. Irregularly shaped nucleus in a cortical cell adjacent to the collapsed epidermis. Fig. 4. A root hair surrounded by hyphae. The epidermal cell to the left has collapsed. Fig. 5. Collapsed root hair and epidermis. Fig. 6. Disorganization of the epidermis, showing fragments of swollen and partly destroyed host cell walls. Fig. 7. A portion of the epidermis and outer cortical layers which have collapsed, showing a hyphal tip entering the cavity of a ruptured cell. Fig. 8. Similar to fig. 7. Note the increased thickness of host cell walls nearest the hyphae. Fig. 9. Hyphae growing between the separated layers of a cell wall in the cortex. Fig. 10. Similar to fig. 9. The cross wall shows separation into layers. Figs. 1–8 ×345; Figs. 9–10 ×760.

growth caused it to thicken into a more or less continuous fungal covering, at first white, but later becoming light-brown or buff. The formation of a complete hyphal envelope was more rapid on roots of corn seedlings than on those of retama. The robust seedling roots of the later species, with their unusually dense covering of stout root hairs, seemed for some reason to offer more resistance to the progress of the mycelium, with the result that two or three days longer were generally required for their complete envelopment.

As a consequence of movements caused by growth of the seedlings, certain parts of the roots were occasionally brought in contact with the cut surfaces of sclerotia for a few hours or longer during the first day after inoculation. In such cases the host tissue at the point of contact usually was injured even before hyphae had begun to grow out from the inoculum. The yellow or brown sunken necrotic areas that developed on the roots after such contacts resembled those which might result from momentarily touching the root with a hot wire.

PATHOLOGICAL HISTOLOGY

Retama. From sections of roots fixed in various stages of the process of hyphal envelopment it was possible to study microscopically the increasing damage to the host, as well as the manner in which invasion by the mycelium occurs. Lesions produced by a few hours' contact of root with sclerotium show in section the collapse of the epidermis and a few of the immediately underying layers of the cortex (figures 1, 2). Close examination of the collapsed cells reveals that some individual walls, which have become greatly increased in thickness and often distorted, may be separated into layers. These walls stain very densely with safranin and gentian violet, with haematoxylin, or with malachite green, according to the stain combination used. In other cases the original cell walls are so tightly compacted that an almost homogeneous dark-staining layer results. If the contact between root and sclerotium is of sufficient duration, the necrotic tissue becomes a substratum for the many hyphae that arise from the inoculum and envelop the dark-staining fragments of root hairs (figure 3).

Sections of roots that had escaped contact with the inoculum but had been attacked subsequently by the mycelium show the hyphae lying irregu-

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Explanation of Figures 11–15

Figs. 11–15. Figs. 11–12 and 14–15. Longitudinal section of roots of seedlings of retama infected with *P. omnivorum.* Fig. 13. Longitudinal section of infected stem of retama seedlings. Fig. 11. Epidermis destroyed and invaded by hyphae; the progressive stages in swelling, collapse, and breakdown of cells is clearly shown. Fig. 12. Hyphae entering a rupture in the cortex caused by the emergence of a lateral root. Fig. 13. Hyphae entering and occupying several cells of the stem. Note distortion and increased thickness of walls near the hyphae. Fig. 14. Hyphae entering a rupture in the root tissue. Fig. 15. Hyphae growing through the cortex of a root. Figs. 11–15 ×345.

larly on the epidermis and among the root hairs. After the weft has thick-
ened considerably, the filaments appear to have surrounded the original
root hairs and to have occupied most of the spaces between these structures
(figure 4). In stained sections of such material the walls of root hairs and
other epidermal cells adjacent to the hyphae have usually absorbed certain
dyes to an extent greater than normal. The Pianeze IIIb technique is espe-
cially well adapted to showing altered staining reactions of this type. The
malachite green of this combination, which is not absorbed heavily by walls
of normal parenchymatous cells, imparts a deep green color to any such
walls that have been exposed to hyphae of *P. omnivorum*. The walls of
epidermal cells in contact with the mycelium appear to be increased in
thickness and at various places are ruptured, distorted, or separated into
visible layers (figure 5). Host cells thus attacked by the mycelium later
appear to be devoid of living matter and finally collapse into irregularly
shaped structures or masses, which usually stain very densely. Continued
fungal action leads to the disintegration of collapsed tissue into frag-
ments of various sizes and shapes, which can often be seen among the fila-
ments of the weft (figure 6). Concurrently with this process, individual
hyphal tips may enter the lumina of cells whose exposed walls have begun
to break down (figures 7, 8).

The action in advance of hyphal entry observed by de Bary (1886)
and subsequently by many investigators for numerous fungi is abundantly
shown in the present material. Six or more layers of cells within the last
hyphae have been found exhibiting various stages in disintegration. Most
examples of this demonstrate a clear succession of stages from the inner-
most cells, showing the beginning of an abnormal staining reaction and
increased thickness of walls, to the outermost, which have broken into
fragments among the hyphae (figure 11).

In addition to invasion of the host by chemical breakdown of its tissues,
the enveloping mycelium also grows into ruptures in the cortex caused by
the emergence of lateral roots (figure 12) and into breaks in the epidermis
produced by mechanical injury (figure 14). This method of entry has been

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Explanation of Figures 16–23

Figs. 16–23. Longitudinal sections (except fig. 22, which is transverse) of corn seed-
lings infected with *P. omnivorum*. Fig. 16. Hyphae aggregated outside the root; the
epidermis is collapsing, and a moribund nucleus is shown in the adjacent cortical cell.
Fig. 17. A hypha entering an outer cell of the root; the walls of the cell entered show
swelling. Fig. 18. Hyphae surrounding the collapsed root hairs. Fig. 19. The epidermis
and outer cortex being broken down by the action of the hyphae. Fig. 20–21. Hyphae
growing into the remains of destroyed root tissue. Fig. 22. Hyphae occupying the cavi-
ties of epidermal and exterior cortical cells. Fig. 23. Similar to fig. 22; note the remains
of host cell walls among the hyphae. Figs. 16–23 ×345.
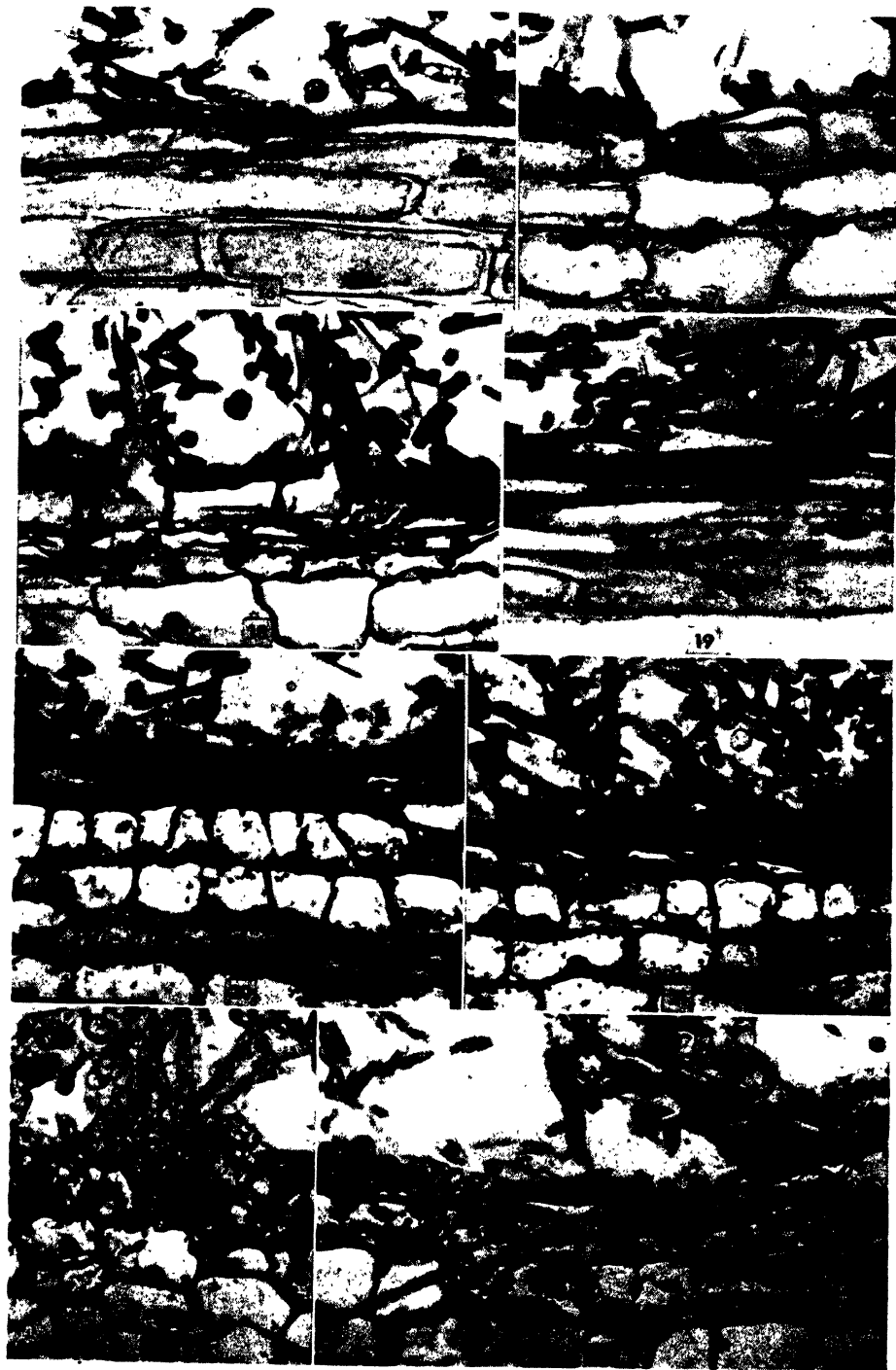
observed by all investigators who have studied the disease from the histological standpoint, including Brinkerhoff (1939) who has recently reported observations on infected roots of pecan trees. There is abundant evidence from infected roots of retama that the fungus, after it has occupied such cavities, continues invasion in the manner described above.

In the earlier description of *Phymatotrichum* root rot of cotton seedlings (Watkins 1938a) two processes were noted by which the mycelial agglomeration attacked the root of its host. The first of these, progressive destruction of host cells from the epidermis to the interior, is identical with the process described above for retama. The second method involved the penetration of individual hyphal tips at various points on the epidermis and the subsequent growth and ramification of these hyphae through and between all cells of the cortex and central cylinder. Most sections of infected roots of retama showed no penetration of individual hyphae into the cortex. In certain preparations, however, the growth of individual hyphae throughout the cortical tissues was seen (figure 15). In these cases the advancing hyphal network did not seem at first to destroy the continuity of host tissues in the interior of the root, but destruction of cells immediately beneath the enveloping weft was observed. Thus a combination of the two types of mycelial action may occur, or one may sometimes lead into the other. The individual hyphae in such sections are often found between separated layers of cell-wall material (figures 9, 10). Roots in advanced stages of infection show the mycelial network in the stele, branching and growing through the vascular tissues.

During the infection of seedlings of retama the stems, as well as the roots, are often surrounded by the mycelium. For the sake of comparison a few pieces of infected stem were fixed and sectioned. In this material the fungus usually brings about the characteristic swelling and disruption of the exterior walls of the epidermis, forming apertures through which the fungus penetrates. While the mycelium is filling the lumen of an invaded cell, the contiguous walls of adjacent cells are broken down in the same way, and the fungus continues its growth longitudinally and centripetally (figure 13).

Corn. An examination of a series of preparations showing progressive stages in the infection of roots of corn seedlings by *P. omnivorum* indicates

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Explantion of Figures 24–27

Figs. 24–27. Sections of roots of corn seedlings infected with *P. omnivorum*. Fig. 24. Hyphae invading cortex; the remains of destroyed tissue appear as irregular dark-staining masses among the hyphae. Longitudinal section. Fig. 25. Hyphae invading the cortex. Transverse section. Fig. 26. Hyphae completely occupying cortical cells; note that in this case the original continuity of cell walls appears essentially unchanged. Transverse section. Fig. 27. Hyphae in the cortex showing host nuclei near hyphae, but apparently normal. Longitudinal section. Figs. 24–27 ×345.
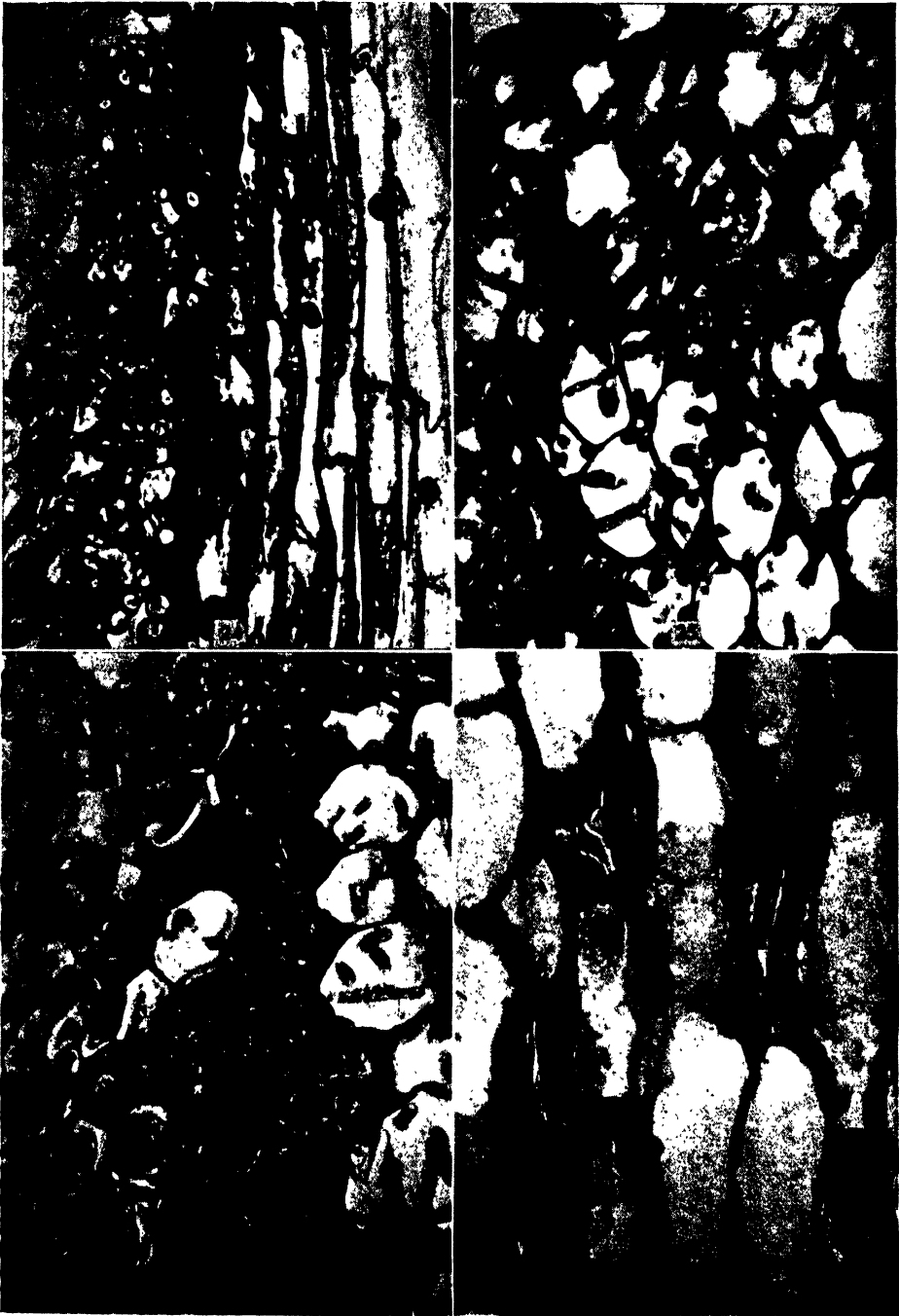
that the process is closely similar to that described in detail above for retama. For that reason only an abbreviated account will be given of infection as it occurs in corn. The action exerted by the enveloping mycelium results in the thickening of walls, collapse of cells, and the final disintegration of tissue in the progressively exposed parts (figures 16–24). The penetration of individual hyphae into the host tissues was observed more frequently in corn than in retama. In such cases the hyphae grow through the cell cavities and intercellular spaces (figure 25) until an irregular mycelial network is formed within the cortex of the root (figures 25, 27). By further growth and ramification the fungus tends to occupy completely the lumina of the invaded cells, producing a solid mass of hyphae partitioned by the remains of the host cell walls, which preserve the outlines of the original continuity of the tissue (figure 26). The complete occupation of host cells progresses from those first invaded, at the periphery of the root, towards the central cylinder. In extremely advanced stages of infection even the outlines of the walls of cortical cells tend to be obliterated, or at least reduced to dark-staining, distorted fragments. By the time this has occurred the various elements of the vascular cylinder are permeated by a network of mycelium.

REACTION OF PROTOPLASTS TO HYPHAL INVASION

The account thus far has dealt exclusively with the action of the fungus on tissues and on cell walls in roots of retama and corn. The protoplasts in roots of both species show a characteristic reaction to the presence of hyphae that is of interest, especially in comparison with the previously described behavior of the cytoplasm and nuclei of cotton roots under similar circumstances. As has been noted before, the protoplasts of cotton roots begin to undergo degenerative changes very shortly after having been exposed to the accumulating mycelium. In retama and corn, on the other hand, the nuclei and cytoplasm seem to be more tolerant of the proximity of the fungus, or perhaps more resistant to its action. Preparations of retama show many nuclei of entirely normal appearance and staining reaction in root hairs completely surrounded by the hyphal weft. The cytoplasm in these cells seems to remain more or less normal until the wall begins to swell; with the degeneration of the wall, however, the cells frequently undergo plasmolysis and the cytoplasm is abnormally granular (figure 4). Simultaneously the capacity of the nucleus to absorb stain increases so markedly that it appears as an opaque body. By the time the cell collapses the protoplast has usually degenerated completely. Nuclei and cytoplasm of normal appearance are frequently seen in cortical cells of retama and corn adjacent to tissue destroyed by mycelial action. Ultimately, however, these protoplasts degenerate in the manner described (figures 1, 2, 3, 11).

In the examples mentioned of the growth of a network of hyphae through the cortex the innermost, advancing margin of the mycelium seems to travel chiefly through the intercellular spaces. Just behind this margin the thickened network includes a few hyphae that have begun to enter the cavities of cells, and with increasing age of the infection the host cells are more and more completely filled with the fungus. In the roots of retama and corn penetrated in this manner some of the most striking cases are found of tolerance of protoplasts to the presence of hyphae. Nuclei and cytoplasm of normal appearance and staining reaction are often found in cells bordering the mycelium (figure 27). In many cells the nuclei fail to show abnormalities even after the cells have been entered by one or more hyphal tips. With the continued proximity of the ever-thickening hyphal network, however, the protoplasts begin to degenerate, and finally there is no evidence of living host material in the invaded cells. Degenerating nuclei are characterized by decreased or increased ability to absorb stains; examples of both are abundant in invaded cortical tissue. It was impossible to determine from the material examined whether these two characteristic reactions represent distinct types of nuclear degeneration, or different stages in the same process.

There is no evidence from the material studied that the roots of retama and corn are ever stimulated by the presence of the fungus to form special structures or tissues to inhibit further invasion by the mycelium.

DISCUSSION

The various attempts to determine the basis of immunity or resistance to *Phymatotrichum* root rot have been reviewed by Ezekiel and Fudge (1938), who attribute the immunity of monocotyledonous plants "at least in part to the presence in the roots of these plants of minute quantities of acidic, ether-soluble substances, possibly organic acids or esters." More recently biochemical studies by Greathouse (1938, 1939; Greathouse and Watkins 1938) have correlated resistance in certain species with the presence of alkaloids or other compounds demonstrated in the roots.

Very young seedlings of retama and corn, growing on nutrient agar, readily become infected after inoculation with a pure culture of *P. omnivorum*. Histological study shows that the disease induced in this manner follows a course very similar to that known for seedlings of cotton, which is highly susceptible. If the immunity of retama and corn in the field is related to the presence in the roots of compounds inhibitory to the growth of the fungus, then it might be suspected that those substances are not yet present in sufficiently toxic concentration in young seedlings to render them immune. On the other hand, if such compounds are normally present in inhibitory concentration during seedling stages, the inhibition is pos-

sibly nullified to a considerable extent by the conditions of the experiment. Under such conditions the pathogen is growing on a favorable medium, while the seedling exists in an unfavorable environment. The preparations examined showed little, if any, consistent evidence of toxicity of host toward pathogen. The hyphae, whether observed in or upon the roots, seemed normal. Experiments designed to permit inoculation of seedlings in soil or sand cultures will possibly determine whether or not the practical immunity of the older plants is possessed to any extent during early seedling stages. The only evidence on this point encountered in the present study is the comparatively great tolerance of the presence of the pathogen by the living host protoplasm, or perhaps the resistance of the latter to the action of fungous exudates. This bespeaks a tendency to a sort of passive resistance, rather than the ability to inhibit aggressively the entrance of the mycelium.

SUMMARY

Young seedlings of retama (*Parkinsonia aculeata* L.) and corn (*Zea Mays* L.) were grown under aseptic conditions in vitro and were inoculated with sclerotia from pure cultures of *Phymatotrichum omnivorum*. Although retama and corn are recorded as being immune from *Phymatotrichum* root rot at maturity under field conditions, they are readily infected in seedling stages in vitro. Histological examination of roots of both species in various stages of infection showed widespread degeneration of cell walls and protoplasts in advance of actual penetration by hyphae. The disorganization and collapse of host cells in this manner proceeds from the epidermis inward, and results finally in the breakdown of the entire cortex. In advanced stages of infection the hyphal network is found in the central cylinder.

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Occurrence of a Disease of Side-oats Grama [1]

R. L. FOWLER AND J. E. WEAVER

The beginning of a disease of *Bouteloua curtipendula*, first observed in 1937 but occurring in alarming proportions in 1939, is of much interest. The fact that this grass has increased greatly during the past six years, from a rank of seventh or eighth among dominants of true prairie to one of the two or three most important species, adds unusual economic interest. Moreover, side-oats grama not only has very wide distribution and is being grown abundantly in grass nurseries of the Soil Conservation Service but also it is one of the most drought-resistant among the best grasses for rejuvenating depleted pastures and reseeding abandoned lands. For these reasons, although the cause of the disease has not been determined, a rather complete account of its occurrence and increase seems warranted.

DISTRIBUTION AND FORMER ABUNDANCE OF SIDE-OATS GRAMA

Bouteloua curtipendula is very widely distributed in the United States and is much used for both hay and forage. It occurs more or less abundantly from Montana to Arizona and is of considerable importance throughout. It ranges eastward to the New England states and southeastward to South Carolina (Hitchcock 1935).

From 1929 to 1933 an extensive survey was made of the percentage composition of the components of true prairie. This study included portions of six states in the Missouri River valley covering a total area of 60,000 square miles (Weaver and Fitzpatrick 1932, 1934). The quadrat method was extensively employed. Among 180 meter quadrats in the little bluestem (*Andropogon scoparius*) type, side-oats grama occurred in 32 per cent and constituted but 0.6 per cent of the basal cover of vegetation. It was found in only 7 per cent of the 155 quadrats examined in the big bluestem (*A. furcatus*) type and composed but 0.1 per cent of the cover. Twenty-five samplings in the much less abundant needle grass type (*Stipa spartea*) revealed an occurrence of 32 per cent but this species constituted only 0.9 per cent of the total vegetation. From these data and extensive observations in the true prairie over the five year period, it was concluded (1932):

"Side-oats grama is scattered widely throughout the prairie in all types of situations, but rarely occurs in great abundance. The largest undisturbed area found that was controlled by this mid grass did not exceed a few square meters. It nearly always occurs as small, isolated, rather open tufts scattered among the other species. A 1 to 3 per cent mixture is common, even on uplands, and it may occur as abundantly as 10 per cent locally. Its habit approaches that of an interstitial species, and

[1] Contribution no. 124 from the Department of Botany, University of Nebraska.

where there is disturbance, such as is caused by erosion on steep banks, etc., it frequently increases in abundance. Quadrats in old roads along ridges sometimes give an abundance ranging from 15 to 60 per cent. It withstands grazing rather well and increases in territory under moderate pasturing. Although nearly always represented in any considerable area, its importance is not great."

When the ravages of the great drought became apparent in 1934, it was decided to select for further study a small group of the 135 prairies formerly examined in western Iowa, where deterioration from drought was small, through southeastern Nebraska to north central Kansas, where drought-damage was very great (Weaver and Albertson 1936). At nine of these stations in Nebraska and Kansas a series of more than 100 permanent sample areas, mostly one square meter in size, was established. An exact record by means of stem counts has been made each year from 1936 to 1939 inclusive (Cf. Robertson 1939). The occurrence of the disease was first observed in these plots by Robertson in July, 1937, in a prairie about 3 miles south of Montrose, Kansas, where it has steadily increased. In the meantime it has been found at many other stations.

<div align="center">INCREASE IN ABUNDANCE FOLLOWING DROUGHT</div>

Great destruction of native grasslands resulted from the most severe drought ever recorded in the prairies of Nebraska and Kansas, especially in 1934 and 1936. All the grasses suffered some loss but especially those with relatively short root systems (4 feet or less in length), notably *Andropogon scoparius, Koeleria cristata, Stipa spartea,* and the invading *Poa pratensis.* Losses varied greatly, but at many of the stations under observation they ranged from 30 to 80 per cent or more. Side-oats grama also lost heavily but in general withstood drought better than the bluestems. Much soil was thus laid bare for invasion. Hordes of short-lived weeds and annual grasses predominated for a year or more, after which western wheat grass (*Agropyron Smithii*) increased at such a rate as literally to take over, in many prairies, most of the land formerly occupied by more mesic grasses.

The great outbreak and spread of wheat grass reached its peak in or before 1938. Since that time this species has still spread somewhat in places where its increase began later than in most prairies, but in nearly all it has waned markedly. This wave of wheat grass was followed closely in many prairies by a similar one of side-oats grama. This resulted from a reclaiming of much drought-denuded territory by side-oats, and by its migration into the wheat-grass area by a process of infiltration. Often it is the chief competitor of the wheat grass. The wide and rapid spread was largely a result of enormous crops of seedlings, which, once established, may develop bunches from 8 to 14 inches in diameter, but it was due partly

to propagation by abundant rhizomes from 2 to 4 inches in length. In some of the prairies this grass now ranks only second in importance to wheat grass; in several it is among the three most abundant grasses; and even where it is of least occurrence it has increased many fold. For example, it now constitutes 40 and 60 per cent, respectively, of the vegetation of the prairies at Carlton and Nelson, Nebraska. This increase under these unusual conditions of intermittent drought has been accompanied by the occurrence and alarming increase of a diseased condition.

EFFECTS OF THE DISEASE AND ITS RATE OF INCREASE

First noted in 1937, the diseased condition was also noticed near Nelson, Nebraska, the following year. During 1939, it was of wide occurrence, being found not only at Valparaiso, Hebron, and Carlton in southeastern Nebraska but also as far west as Holdrege and Edison. In Kansas it occurred at Belleville and as far southeast as Melvern, south of Topeka. The diseased plants occur in scattered patches, sometimes throughout the prairie, but are more prevalent in drier places. The size of the patches varies from a few square inches to one or more square rods, the destruction wrought often including two-thirds of the plants and being so great that the larger affected areas are conspicuous at a distance of several rods.

Symptoms of the disease, based on field observations, include the appearance in early spring of rosette-like clumps or portions of bunches which contain tillers in very large numbers, often 70 or more per square centimeter. The rosetted plants or portions of plants do not elongate normally; many are only an inch or two high, and the foliage seldom attains a height exceeding 3 or 4 inches. The stem bases develop a distinctly reddish color. The leaves are dwarfed to only one-third or less their usual width. The general appearance reminds one strongly of mosaic (virus) disease of wheat (McKinney 1937). The leaves are yellowish-green in color and turn brown after death. The brown color is very different from that of normal dead leaves, which bleach almost white. Flower-stalks, if any, show marked reduction in number, often to 20 per cent, and attain only about two-thirds the normal height (figures 1 and 2). Death and browning of small bunches or portions of larger ones may occur early in June, but later many more plants or other parts of the bunches become affected. In the Nelson prairie, which is composed of 60 per cent side-oats grama, approximately 30 per cent of the plants throughout the prairie were diseased (figure 3).

IMPORTANCE OF THE GRASS IN RANGES AND IN SOIL CONSERVATION

This is one of the largest species of grama grass. It is a mid grass of the bunch habit despite the presence of rhizomes, and reaches a height of from 1 to 4 feet. The plants produce much foliage, and because of their leafiness the species is prized both for forage and hay. Although it fur-
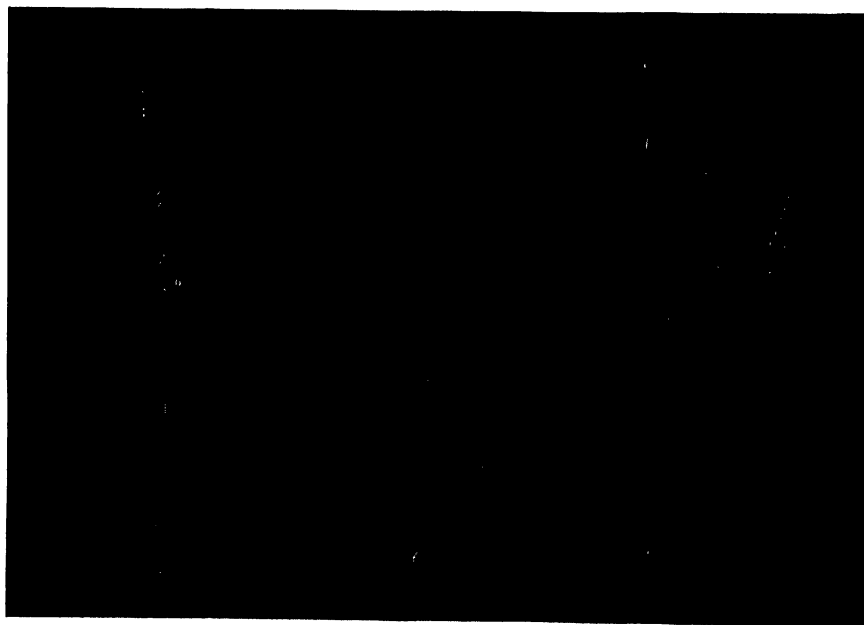
Fig. 1. Detail of a small portion of a widely affected area of pure side-oats grama at Nelson, Nebraska, on August 15, 1939. Note the abundant, narrow, dead leaves and the few remaining broad and erect live ones. There are no flower stalks.

Fig. 2. Normal healthy plants of side-oats grama (ends) about 3 feet tall and two groups of diseased ones (center) with short, fine, dead leaves and few or no flower stalks. August 15, 1939.
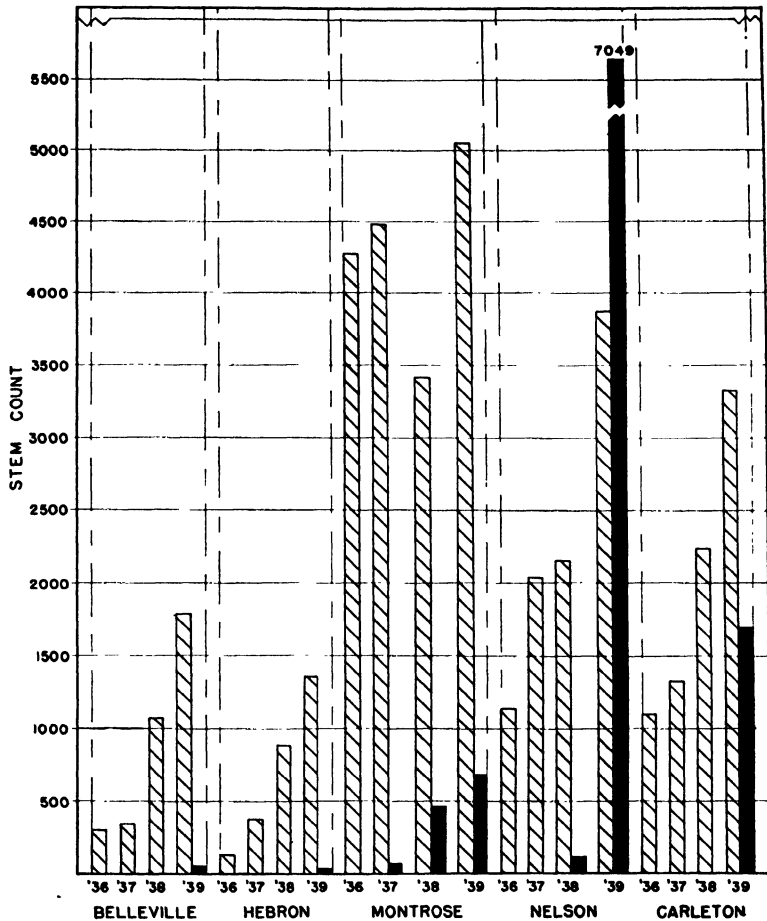
Fig. 3. Rate of increase in number of normal stems of side-oats grama (right hatch) and diseased stems (black) during 4 years. These data are from permanent meter quadrats which contained diseased plants during the period. of observation. Percentage of diseased stems in 1939 was 2.9 at Belleville, 2.3 at Hebron, and 33.6 at Carleton. At Montrose, diseased stems were 1.4 per cent in 1937, 12.1 per cent in 1938, and 11.8 per cent in 1939. At Nelson 5.2 per cent were diseased in 1938 but 64.5 per cent in 1939.

nishes forage both summer and winter, the dried grass is of rather low palatability compared with many other gramas. Nor does the good palatability of the green plants include the stems, which are rather inedible and often left standing after the foliage has been eaten.

Its wide range of distribution shows its considerable adaptability. It grows well, and often in pure stands, on dry steep banks or in thin, rocky soil or as a component of luxuriant prairie on fertile loams. This wide adaptability to habitat, its large size, vigorous, rather early growth, drought resistance, and good seeding habits combine to make it a desirable

grass for domestication and use in grass mixtures in reseeding ranges and abandoned lands. It is known as a grass that will control erosion, the strongly branched, deep root system firmly anchoring the plants in the dense sod which develops under artificial seeding. It is recommended in a mixture with blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*) for growth on drought-bared lands of the semiarid west (Cornelius 1939).

As pointed out by Cardon (1937), the extent to which disease may affect the carrying capacity and nutritive value of pasture grasses has not yet been determined on American ranges. When further studies are made it may be found that disease resistance will take on greater importance, with resistance to winter killing, to insect injury, and to drought.

Whether this disease is caused by insect damage, fungi, bacteria, a virus, or is physiological in character is unknown.[1] It seems reasonable that the extreme conditions of environment resulting from the years of drought may have been a contributing factor. The normal mulch of litter has often been replaced by bare soil (figure 1). The wide spacing of the plants permits full insolation to their base, and results in extremes of soil temperatures. The great quantities of dead underground materials from vegetation overcome by drought have temporarily modified organic content of soil, as is witnessed by a highly abnormal number of saprophytic fungi during wet weather. Other factors, notably extremes in water content of soil, have been equally pronounced.

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[1] Research on the identification of this disease from plants furnished by the writers is being conducted by Dr. J. H. Jensen, University of Nebraska, College of Agriculture.

Supplementary Notes on American Labiatae

CARL EPLING

The past year has witnessed unusual botanical exploration in tropical America and has resulted in the accumulation of a series of undescribed species of Labiatae, as well as a number of significant extensions of ranges. It is the purpose of the present paper to record these.

Most of these records pertain to *Salvia* subgenus *Calosphace* and hence may be taken as supplementary to a recent paper by the author upon that subject (Rep. Spec. Nov. Beih. **110.** 1939). For convenience, the numbering of species and sections, as well as occasional page numbers which are cited, correspond to the numbering in the paper cited.

The collections most referred to are those made by G. B. Hinton, L. Rowntree, C. W. Penland, C. H. Muller, C. L. Lundell, H. L. Gentry, E. Matuda, L. A. Kenoyer, F. Shreve, P. N. Standley, and R. E. Woodson, Jr.

Trichostema mexicanum Epling, sp. nov. Herba perennis parva altitudine 15–30 cm., caudice lignoso in basi ramoso caulibus numerosis erectis gracilibus utrimque glandulosis capitatis et sessilibus puberulis ut videtur viscidis; foliorum laminis ovalibus vel ellipticis magnam partem circiter 1 cm. longis subsessilibus, integris, utrimque sparse hirtellis et dense glandulosis; floribus in racemis gracilibus dispositis, pedicellis arcuatis 1.5–3 cm. longis internodia aequantibus vel superantibus elatis; calycibus florentibus 3.5 mm. longis, extus dense et minute glandulosis, laciniis tubum subaequantibus anguste ovatis acutis, in maturitate tubo paulo aucto; corollis cyaneis vix 5 mm. longis; staminibus circiter 8 mm. longis; nuculis glandulosis.

MEXICO. Coahuila: Puerto de San Lazaro, Sierra de San Lozan, Mun. de Castaños, *C. H. Muller 3055* (type, Univ. Calif., L. A.). In habit this species suggests a diminished form of *T. arizonicum*. It differs from that species particularly in pubescence, the smaller flowers and the simple racemes.

CATOPHERIA CAPITATA Benth. GUATEMALA. Alta Verapaz: Forest above Rio Chiacte, 6800 ft., *C. L. Wilson* (Field Mus.).

HYPTIS OBLONGIFOLIA Benth. Widely spread from Sinaloa to Panama, this species appears to be fairly stable. It is frequently collected in Michoacan and was recently gathered there near Coalcoman in the Sierra Naranjillo by Hinton (*No. 12661*). This specimen is average, with leaves 5–6 cm. long, borne on petioles about 1 cm. long. However, Hinton gathered another plant (*No. 12702*) at Puerto Zarzamora near Coalcoman which appears to be *H. arborescens* Epling, described from Mt. El Viejo, Nicara-

gua. The leaves are 13 cm. long and correspondingly wide and are borne on petioles about 4 cm. long. The tomentum is much thinner. It would appear therefore either that *H. arborescens* has a remarkable distribution or, as seems more probable, is an extreme variant of *H. oblongifolia*. In any case the discontinuity in leaf habit is abrupt and marked.

H. SUBTILIS Epling. (*H. perpulchra* Epl.) MEXICO. Michoacan: Coalcoman, Aquila, *Hinton 12605*. Comparison with the type of *S. subtilis* shows these species to be conspecific.

H. IODANTHA Epling. MEXICO. Colima: Paso del Rio, *G. M. Emrick 209*. Michoacan: Maguila, *G. M. Emrick 36*. Apparently glabrate forms of this species.

Hyptis intermedia Epling, sp. nov. (*Cephalohyptis*.) Herba suffruticosa dumetorum humidorum erecta altitudine ad 1 m. et ultra, caulibus obtuse quadratis utrimque pilis ascendentibus appresso-hirsutis; foliorum laminis 6–10 cm. longis, 2–3 cm. rarius 4 cm. latis, ellipticis vel ovato-ellipticis, in apice acutiusculis in basi cuneatis vel acuminatis et in petiolos vix 1 cm. longos marginatos attenuatis etiam subsessilibus, utrimque hirsutis vel villosis, margine serrata; capitulis demum 10–12 mm. diametro compactis, in foliorum supremorum axillis pedunculis saepius 10–12 mm. longis rarius 5 mm. longis elatis, bracteis ovatolanceolatis vel ovatis 3–4 mm. longis subtentis; calycum florentium 1.5–1.7 mm. longis, dentibus subaequantibus anguste deltoideis acutiusculis, in maturitate tubo vix 3 mm. longo, dentibus paulo auctis vix conniventibus; corollarum albidarum tubo vix 2.5 mm. longo; nuculis obovatis vix 1 mm. longis.

GUATEMALA. Alta Verapaz: Saquija, near Coban, 1200 m., *Standley 70177a, 70195* (type, Field Mus.) ; Chelac, near Carcha, 1500 m., *Standley 70393*; Coban, *Standley 71485*; Pancajche, 360 m., *Standley 70647*.

This species is seemingly intermediate with *H. personata* Epling and *H. obtusiflora* Presl, the former widespread in Colombia, the latter ranging from Colombia to Bolivia. All are similar in habit, aspect and pubescence. This species more nearly suggests the latter in that the calyx teeth are more blunt. The flowers and capitula of this species are larger, on longer pedicels and the calyx teeth are not connivent in fruit as in *S. obtusiflora*. It seems remarkable that, occurring as it does near Coban, it has not been previously collected. It might be confused with *S. lanceolata*, but the more conspicuous lanceolate bracts and larger flowers should readily distinguish that species. In Guatemala *S. lanceolata* is known only from Puerto Barrios (*Standley 24759*), perhaps as an introduced weed.

H. OBTUSIFLORA Presl. COLOMBIA. El Choco: Andagoya, 70–100 m., *Killip 35070*.

H. BRACHIATA Briq. COLOMBIA. Los Llanos, Rio Casanare, 130 m., woods and sabana, *Cuatrecasas 3806*; Rio Meta, 140 m., sabana, *Cuatrecasas 4387*.

ERIOPE CRASSIPES Benth. COLOMBIA. Boyaca: Los Llanos, *Haught 2655*.

COLEUS ATROPURPUREUS Benth. COLOMBIA. El Choco: Andagoya, *Killip 35077*.

STACHYS LAMIOIDES Benth. ECUADOR. Near Bolivar, Hacienda Talahua, 2900 m., *Penland & Summers 668*. Canar: Tipococho, 3200 m., *Penland & Summers 1019*.

S. MICHELIANA Briq. ECUADOR. Tungurahua: Between Hacienda San Francisco and Rio Margarjitas, *Penland and Summers 177*.

S. PUSILLA (Wedd.) Briq. ECUADOR. Bolivar: 3100 m., Hacienda Talahua, *Penland & Summers 603*.

S. DEBILIS Kunth. ECUADOR. Pichincha: Uymubicho, 2800 m., *Penland and Summers 947*. Azuay: Banos near Cuenca, 2600 m., *Penland and Summers 1059*.

S. ELLIPTICA Kunth. ECUADOR. Bolivar: Hacienda Talahua, 3100 m., *Penland and Summers 679*.

Lepechinia caulescens (Ort.) Epling, comb. nov. *Horminum caulescens* Ort., Hort. Matr. Dec. 63. 1797. *Lepechinia spicata* Willd., Hort. Berol. 1: 21. *t. 21*. 1806. *Ulricia pyramidata* Jacq. ex Steud. Nom. ed. 1, 862. 1821. GUATEMALA. Chimaltenango: Barranco de La Sierra, *Standley 61600*; Finca La Alameda, *Standley 59154*. Quezaltenango: Cerro La Pedrera, *Standley 65557*.

L. SCHIEDEANA (Schlect.) Vatke, Verh. Bot. Ver. Brandenb. **17:** Sitz.-ber. 36. 1875. *Stachys Schiedeana* Schlect. in Linnaea 7: 398. 1832. *Sphacele procumbens* Benth., Lab. Gen. et Sp. 415. 1834. *Sphacele alpina* Oerst. in Vidensk. Meddel. Kjoeb. 1853: 36. *Lepechinia alpina* Standley in Field Mus. Pub. Bot. **18:** 1023. 1938. GUATEMALA. Chimaltenango: Cerro de Tecpam, *Standley 61016*, 58799. Huehuetenango: Sierra de los Cuchumanes, *Standley 65611*.

L. **Nelsonii** (Fern.) Epling, comb. nov. *Hyptis Nelsonii* Fern. in Proc. Am. Acad. **35:** 566. 1900. *Sphacele pinetorum* Standley in Field Mus. Pub. Bot. **4:** 257–258. 1929. Recently collected in Jalisco, Guerrero and Mexico by Mexia and Hinton.

L. **mexicana** (S. Schau.) Epling, comb. nov. *Sphacele mexicana* S. Schau. in Linnaea **20:** 707. 1847. MEXICO. Oaxaca: Los Naranjos, *Purpus 3295* (distributed as *Hyptis*).

L. **hastata** (Gray) Epling, comb. nov. *Sphacele hastata* Gray in Proc. Am. Acad. **5:** 341. 1862. MEXICO. Baja California: La Laguna, Sierra Laguna, oak pine forest, 6000 ft., *Gentry 4397, 4397a*.

L. **Urbani** (Briq.) Epling, comb. nov. *Sphacele Urbani* Briq. in Bull. Herb. Boiss. **5:** 1014. 1897. HAITI. Massif de la Selle, Morne La Visite, *Ekman 1442*.

CHAUNOSTOMA MECISTANDRUM J. D. Smith. MEXICO. Chiapas: Mt. Ovando, *Matuda 2649, 3915*. The corolla is white, the calyces blue. Known previously only from the type locality in Guatemala, Santa Rosa, near Buena Vista. The nutlets, the nature and development of the calyx, the branched pubescence and habit of the foliage, all relate this remarkable plant to *Lepechinia*. The nutlets are unlike any other American genus save that. The cauline inflorescence is unique.

Hesperozygis bella Epling, sp. nov. (*Muellerostachys*.) Herba perennis suffruticosa caespitosa laxa caulibus procumbentibus pluribus e caudice lignoso 15–30 cm. longis plerumque simplicibus plus minusve pilis ascendentibus crispis hirtellis; foliorum laminis coriaceis ellipticis interdum oblanceolatis, 1–2 cm. longis, integerrimis glaberrimis, saepe purpureis et subtus pallidioribus, petiolis 1–2 mm. longis elatis; cymulis 1–6-floribus in foliorum superiorum dispositis interdum subspicatis; calycum purpureorum tubo 5–6.5 mm. longo solum ad venas sparse hirtello, sub annulo constricto, labia superiore circiter 2 mm. longa, dentibus deltoideis circiter 1 mm. longis recurvis; inferioris dentibus pungentibus 4 mm. longis, ciliolatis, annulo denso in tubo incluso; corollarum pallide rosearum maculatarum tubo 8–10 mm. longo intus hirtello.

MEXICO. Jalisco: San Sebastian, 1500 m., *Mexia 1514* (type, Univ. Calif., Berk.). It should be noted that unlike those of the other species, the upper teeth of this are joined to the middle. In stamens it is similar to the other species but unlike *H. ciliolata* in which they are exserted beyond the upper lip.

SATUREJA MUTABILIS Epling. ECUADOR. Azuay: near Cuenca, 2600 m., *Penland and Summers 1049*. Either this species exists in two well-defined forms or else two similar species are represented, one with elliptical leaves acute at the apex and narrowed at the base, 1–2 cm. long, and one in which the leaves are broadly ovate or deltoid-ovate and truncate at the base. There are no perceptible differences in pubescence nor in habit of the flowers, save that the calyces of the elliptical form appear to be thinner with sharper teeth. From the material available it is difficult to reach a conclusion. Both types appear on the Jameson sheets, collected presumably near Quito. A specimen collected by Heilborn (No. 520) on Rio Machaugua near Quito, is the elliptical form. The present specimen is the truncate form. What is seemingly this species, the form with elliptical leaves, has only now come to hand from COLOMBIA. Boyaca: Valle de Cocuy, *Cuatre-casas 1276*.

S. NUBIGENA (Kunth) Briq. ECUADOR. Tungurahua: Paramo de Minza Chica, 3800 m., *Penland & Summers 334*. Carchi: Nudo de Boliche Vola-dero, 3900 m., *Penland & Summers 918*.

S. BROWNEI (Sw.) Briq. COLOMBIA. Tolima: Quindio Highway, *Killip & Varela 34528*.

HEDEOMA PATRINUM Stewart. MEXICO. Coahuila: Sierra Mojada, Cañon de San Salvador, Mun. de Sierra Mojada, *C. H. Muller 3302.*

SALVIA SECT. AUBIBERTIA

S. PACHYPHYLLA Epling. ARIZONA. Polacca-Winslow Road, *A. F. Whiting.* 25 miles north of Winslow, valley of Little San Francisco River, 5600 feet, *Peebles 14406.*

S. MOHAVENSIS Greene. NEVADA. Clark County: Boulder Dam, *J. P. Hester.* ARIZONA. Mohave County: Jack Pot Spring, Needles Mts., *F. Shreve.*

S. FUNEREA M. E. Jones. CALIFORNIA. Echo Canyon, Funeral Range, Death Valley, *P. Train.*

SALVIA SECT. CALOSPHACE

9. S. PINGUIFOLIA W. & S. ARIZONA. Maricopa County: Sierra Estrella, *E. G. Smith 12947;* Fish Creek Canyon, *Epling and Pratt.*

20. S. GOLDMANII Fern. It should be observed that the mature calyx pictured in Pl. 2, fig. 3, is the calyx of *S. ballotaeflora* and not that of *S. Goldmanii.*

27. S. CLINOPODIOIDES Kunth. MEXICO. Michoacan: between Toluca and Zitacuaro, 8000 ft., *Rowntree 175.*

28. S. ALBOCAERULEA Lind. MEXICO. Michoacan: Zitacuaro-Aputzio. 2350 m., *Hinton 13448.*

29a. **Salvia pseudoincisa** Epling, sp. nov. (*Caducae.*) Herba annua pusilla ramosa altitudine 30 cm. caulibus utrimque pilis minutis appressis hirtellis nullomodo glandulosis; foliorum laminis oblongo-ellipticis circiter 3 cm. longis circiter 1 cm. latis ut videtur obtusis et subintegris in basi ad petiolos graciles 1–15 cm. longos angustatis, utrimque sparse hirtellis; floribus saepius solitariis et oppositis bracteis lanceolatis 2–3 mm. longis glabris subperstatis subtentis, glomerulis inter se 1–3 cm. distantibus; calycibus florentibus 5–6 mm. longis, extus ad venas appresso-hirtellis, nullomodo glandulosis, in maturitate 8 mm. longis, labiis hiantibus, superiore 5-venis; corollarum (?) albarum tubo 4.5 mm. longo, labia superiore 2 mm. alta, inferiore circiter 4 mm. longa; stylo hirtello.

MEXICO. Tamaulipas: Jaumave, 620 m., *Viereck 859* (type, U. S. Natl. Herb.). Apparently allied to *Salvia subincisa* from which it may be distinguished as follows (p. 33):

Caules superne et calyces glandulosi; styli glabri;
   bracteia caduca glandulosa........................ 29. *S. subincisa*
Caules superne et calyces appresso-hirtelli, nullomodo
   glandulosi; styli hirtelli; bractea subperstata glabra.. 29a. *S. pseudoincisa*

Because of the persistent or subpersistent bracts this species will not be found in the sectional key under *Caducae*, but would be looked for somewhere near *Microsphace, Cucullatae,* or *Uliginosae* (p. 9).

32a. Salvia exilis Epling, sp. nov. (*Lavanduloideae.*) Herba glabra perennis exilis altitudine ad 1.25 m. caulibus gracillimis e caudice lignoso superne ramosis internodiis elongatis 5–15 cm. longis; foliorum laminis oblongo-ellipticis 2.5–5 cm. longis, 6–8 mm. latis, in apice obtusis in basi ad petiolos 5–10 mm. longos extenuatis, paginis ambabus glabris inferiore pallidiore venulosa marginibus integris; floribus 3–6 in verticillastris approximatis inter se 3–10 mm. distantibus in spicis laxis 3–6 cm. longis longe pedunculatis dispositis; calycibus florentibus 3 mm. longis extus ad venas sparse appresso-hirtellis, in maturitate paulo auctis ut videtur magnam partem deflexis; corollarum tubo 4 mm. longo, labia superiore 2.5 mm. alta.

MEXICO. Guerrero: Reyes, Sierra Madre del Sur, Petlacala, on pine forested slope, 1800–1950 m., *Mexia 9097* (type, Univ. Calif., L. A.). Mina, Toro Muerto, in pine forest, 2480 m., *Hinton 11093.*

32b. Salvia subobscura Epling, sp. nov. (*Lavanduloideae.*) Herba perennis ut videtur diffusa altitudine ad 1 m. caulibus gracilibus laxe ramosis utrimque pilis decurvis sparse pubescentibus internodiis plerumque 5–8 cm. longis; foliorum laminis ovalibus magnam partem 1.5–2.5 cm. longis 8–12 mm. latis, in apice acutis in basi rotundato-angustatis petiolis 2–3 mm. longis elatis pagina superiore sparse hirtella, inferiore pilis eis ramorum similibus pubescentibus, marginibus supra medium crenato-serratis; floribus 3–6 in verticillastris approximatis inter se 3–6 mm. distantibus in spicis laxis 6–7 cm. longis subpedunculatis dispositis; calycibus florentibus 4 mm. longis extus utrimque pilis appressis hirtellis, in maturitate vix auctis ut videtur magnam partem deflexis; corollarum tubo 4 mm. longo, labia superiore 2 mm. alta.

MEXICO. Michoacan: Coalcoman, Villa Victoria, 1340 m. in pine forest, *Hinton 12570* (type, Univ. Calif., L. A.).

The section *Lavanduloideae* is one of the most clearly marked of any of the sections of *Salvia* both in habit and floral structure. Within the section, however, specific lines are difficult to ascertain, particularly with the dearth of available material. It is therefore not without misgivings that I have described these species as such. In the key to the section, *S. subobscura* would be sought either near *S. guadalajarensis* which it most resembles, or near *S. lavanduloides.* From either of these it may be distinguished by the small flowers. *S. exilis* would probably be sought near *S. guadalajarensis.* In habit it strongly suggests *S. Teresae* or *S. scaposa,* save that the leaves are evenly distributed along the stem. From all of these it may be distinguished by the small flowers.

39. S. LONGIFOLIA Willd. What seems to be this species has been collected by Rowntree (11. XI. 1938) 30 mi. east of Morelia, Michoacan, 7500 ft.

41. S. LAVANDULOIDES Kunth. GUATEMALA. Quezaltenango: Olintepeque, 2550–2850 m., *Standley 65970*. Huehuetenango: Rio Pucal, 1775 m., *Standley 65841*. Solola: Los Encuentros, 2400–2850 m., *Standley 62346*. Totonicapan: Cumbre del Aire, 3000–3450 m., *Standley 65885*.

Salvia fratrum Standley, described from San José, Costa Rica, appears to be a depauperate specimen of this species. The type is hardly adequate for a conclusion.

What is apparently a form of this species with the pubescence of the lower leaf surface finer, more dense, and white has been collected by Hinton (*11953, 13474, 13557*) in Michoacan, district of Zitacuaro; one is an albino.

53. S. DASYCALYX Fern. Known previously from an inadequate specimen thought to have been collected in Guerrero. Collected now by Hinton in Guerrero, distr. Montes de Oca, near San Antonio (*14016*), distr. Mina, near Aguazarca Filo (*11321*) and Toro Muerto, Camp Morado (*11236*), and in Michoacan, distr. Coalcoman, in Sierra Torricillas (*12769, 12411*) and at Coalcoman (*13610, 12930*). The flowers are actually smaller than those of *S. thyrsiflora*, as previously described, and the calyces are clothed with coarser hair which is largely eglandular and tends to curl upward. The calyx limb is shorter than that of *S. thyrsiflora* and the hairs on the lower surface of the leaves coarser and less dense.

57. S. CORRUGATA Vahl. ECUADOR. Bolivia: Hacienda Talahua, 2000 m., *Penland and Summers 539*.

11a. SECT. LANATAE

Herbae perennes caulibus ut videtur e caudice lignoso ascendentibus utrimque albo-lanatae; foliorum laminis late ovatis crassiusculis corrugatis breviter petiolatis; floribus oppositis in racemis terminalibus brevibus dispositis bracteis caducis subtentis; calycum labia superiore 5-venis quam inferior paulo longiore; corollarum rosearum tubo ad basim invaginato et papillis parvis inconspicuis quatuor intus ornato, labia inferiore quam galea duplo longiore; staminibus ad fauces positis, gubernaculo in dentem obscurum assurgenti-dilato; styli utrimque pilosi ramo postico quam anticus duplo longiore; gynobasis cornu ovula paulo superante.

59a. **Salvia leucochlamys** Epling, sp. nov. (*Lanatae.*) Herba perennis altitudine circiter 30 cm., caulibus utrimque incano-hirsutis nullomodo glandulosis, internodiis quam folia saepius brevioribus; foliorum laminis late ovatis 1.5–2 cm. longis, in apice obtusis vel breviter acutiusculis, in basi truncato-subcordatis, pagina superiore cinerea molliter hirsuta corrugata, inferiore densissime albotomentella cretata, marginibus crenulatis, petiolis 3–5 mm. longis;

calycibus florentibus incano-hirsutis nullomodo glandulosis 10 mm. longis; corollarum roseo-purpurearum tubo 12 mm. longo supra basim 4 mm. leniter invaginato et papillato, labia superiore 6–7 mm. alta, inferiore 13 mm. longa, lacinia media pro rata grandiore 8 mm. lata; staminum connectivo 10 mm. longo ad medium connexo, gubernaculo 3.5 mm. longo.

GUATEMALA. Huehuetenango: Above Chiantla in Sierra de los Cuchumatanes, *Standley 65650* (type, Field Mus.).

This species clearly belongs to that part of the genus which has the lower portion of the connective developed into an assurgent tooth, weakly so in this species but still clear. However, it is unique in the sense that the flower color is purple rather than blue and, with the exception of *Corrugatae*, has an invaginate corolla tube. In habit it is not unlike that section, but the upper lip of the calyx is 5-veined rather than seven, the style is hirsute on both margins and the flowers, rather than being in dense globerules, are opposite. The sessile glands on calyx and corolla which occur in most of the sections which are characterized by this type of stamen, are wanting. It apparently occurs with *S. Urica.*

In the sectional key it may be distinguished as follows (p. 10):

G. Plantae andinae foliis corrugatis 11. *Corrugatae* GG. Plantae mexicanae H. Folia ad 2 cm. longa plus minusve corrugata superne cinereo-hirsuta, subtus densissime albotomentella 11a. *Lanatae* HH. Folia glabra elliptica 10–20 cm. longa 6. *Fernaldia.*

62. S. ARIZONICA Gray. ARIZONA. Turkey Flat, Pinaleno Mts., *Kearney and Peebles 14115.*

63. S. FORRERI Greene. MEXICO. Chihuahua: Salto de Babicora, *Le Sueur 1383.*

64a. **Salvia cyanicephala** Epling, sp. nov. (*Uliginosae.*) Suffrutex altitudine ad 1 m. caulibus gracilibus superne pilis decurvis sparse villosis et longioribus extensis gracilibus nullomodo glandulosis ornatis; foliorum laminis deltoideo-oblongis magnam partem 4–5 cm. longis, circiter 1.5 cm. latis, in apice obtusis, in basi subtruncatis vel late cuneatis, marginibus crenulatis, pagina superiore viride hirtella, inferiore albo-tomentosa, petiolis ad 1 cm. longis elatis; floribus circiter tribus in verticillastris bracteis cyaneis acuminatis deciduis molliter et sparse hirsutis subtentis, glomerulis inter se .5–2 cm. distantibus in spicis interruptis 10–15 longis approximatis; calycibus florentibus 7 mm. longis, labiis tubum aequantibus, extus pilis gracilibus molliter hirsutis, in maturitate paulo auctis; corollarum tubo 8 mm. longo, labia superiore 5 mm. alta.

MEXICO. Michoacan: Coalcoman, Sierra Torricillas in quercetis, 2400 m., *Hinton 12792* (type, Univ. Calif., L. A.). Very similar to *S. setulosa* with which it may prove to be conspecific. It may be distinguished from

S. setulosa by the dense tomentum on the lower leaf surface, the hirsute bracts and narrow leaves.

68. S. GLECHOMAEFOLIA Kunth. MEXICO. Hidalgo: Jacala, *Kenoyer 868; O. E. White 34.*

69. S. PRUNELLOIDES Kunth. MEXICO. Morelos: Cuernavaca, *Kenoyer A211.*

75a. **Salvia tricuspis** Epling, sp. nov. (*Uliginosae.*) Suffrutex altitudine ad 1 m. caulibus gracilibus superne pilis brevibus decurvis pubescentibus et praesertim inter flores extensis longioribus glandulosis plus minusve viscidis; foliorum laminis oblongo-ellipticis magnam partem 6–8 cm. longis, 2–3 cm. latis sat tenuibus utrimque acuminatis subsessilibus serrulatis, pagina superiore hirtella, inferiore venulosa ad venas villosula; floribus circiter tribus in verticillastris bracteis caducissimis subtentis glomerulis inter se 1–3 cm. distantibus in spicis interruptis 10–15 cm. longis dispositis; calycibus florentibus 5–6 mm. longis, extus pilis brevibus et longioribus glandulosis viscidis, labiis hiantibus cuspidibus 1–1.5 mm. longis ornatis; corollarum tubo 4 mm. longo intus rugis binis ornato, labia superiore 3.5 mm. alta; stylo postice pilis fuscis villoso.

MEXICO. Guerrero: Mina, Aguazarco Filo, *Hinton 11260* (type, Univ. Calif., L. A.). May be distinguished from *S. rostellata* by the glandular inflorescence.

79. S. ASSURGENS Kunth. MEXICO. Michoacan: Zitacuaro-Zirahuato, 1920 m. *Hinton 11960, 11858.* ? Michoacan: between Carapa and Zamora, 5000 ft., *Rowntree 222.*

103. S. PICHINCHENSIS Benth. ECUADOR. Bolivar: Hacienda Talahua, 3000 m., *Penland and Summers 550.*

105. S. MACROSTACHYA Kunth. ECUADOR. Chimborazo: Calere, beyond San Juan toward Tilelac, 3300 m., *Penland and Summers 507.*

113. S. SCUTELLARIOIDES Kunth. ECUADOR. Imbabura: Lake Cuicocha, 3000 m., *Penland and Summers 777.*

119. S. PATENS Cav. COSTA RICA. Zarcero, *Austin Smith* (? naturalized).

119b. **Salvia viscidifolia** Epling, sp. nov. (*Blakea.*) Herba perennis radicibus fusiformibus caulibus paucis erectis altitudine ad 60 cm. utrimque pilis extensis longioribus mollibus viscidis villosis; foliorum laminis sat tenuibus sessilibus infimis deltoideo-ovatis (vel ? ovatis) 3–5 cm. longis, mediis 5–8 cm. longis anguste ovatis acutis in basi rotundatis supremis similibus minoribus omnium marginibus irregulariter duplicato-dentatis paginis ambabus viscidopilosis, inferiore pallidiore; floribus oppositis, bracteis lanceolatis 5–6 mm. longis subtentis, glomerulis inter se 1–2 cm. distantibus in racemis laxis viscidis dispositis; calycibus florentibus 7.5 mm. longis, extus viscido-pilosis, labia superiore sub-5-venis, trimucronata, in maturitate 10 mm. longis; corollarum

tubo 10–11 mm. longo, ad basim invaginato, labia superiore subaequilonga, inferiore duplo longiore patente; staminibus e labia 10 mm. exsertis.

MEXICO. Guerrero: Mina, Rio Frio Diamantes, 2100 m., wet ground in pine forest, *Hinton 10725* (type, Univ. Calif., L. A.). Michoacan: Coalcoman, Sierra Torricillas in llano, 2200 m., *Hinton 12369; 2150*. Barroloso, in pinetis, *Hinton 15091*. Because of the exserted stamens this species would be sought in the Key to Sections either under *Standleyana* or *Hastatae*. However, the conformation of the corolla and stamens is that of *Blakea*. The habit is remarkably like that of *S. subpatens* from which this species may be distinguished by the smaller flowers and viscid pubescence, as well as the exserted stamens.

131. S. HISPANICA L. ECUADOR. Tungurahua: Banos, 1750 m., *Penland and Summers 69*. (Introduced.)

134. S. HIRTELLA Vahl. ECUADOR. Canar: Ingapirca ruins, 3000 m., *Penland and Summers 1037*.

139. S. ORTHOSTACHYS Epl. COLOMBIA. Boyaca: Valle de la Uvita, *Cuatrecasas 1145*.

144. S. QUITENSIS Benth. ECUADOR. Azuay: Sayausi to Cajas, 3000 m., *Penland and Summers 1072*.

173. S. CINNABARINA M. & G. MEXICO. Chiapas: Mt. Tacana, *Matuda 2306*. GUATEMALA. Totonicapan: Cumbre del Aire, 3000–3450 m., *Standley 65849*. San Marcos: Chamac, 2250 m., *Standley 66186*. San Antonio, 2700 m., *Standley 66094*. Guatemala: San Juan Sacatepequez, 1800 m., *Standley 59242*.

174. S. ELEGANS Vahl var. SONORENSIS Fern. MEXICO. Chihuahua: Rio Aros, *H. Le Sueur*.

175a. SALVIA LUNDELLII Epling (? *Iodophyllae*.) BRITISH HONDURAS. El Cayo: Arenal, in clearing on bank of Mopan R., *Lundell 6165* (type, Univ. Mich.); Cohune Ridge, Chalillo Crossing trail, in high forest, *Lundell 6527*; Camp 32, B. H., Guatemala Survey, 2700 ft., *Schiff s-632*. In habit this species is very like *Salvia bella* of Costa Rica, which I have referred to section *Flexuosae*. However, its flower structure, save for the fact that the tube is epapillate, suggests more strongly the section *Iodophyllae*. Definite assignment cannot be made until more adequate collections are made of the flowers.

38a. SECT. PEDICELLATA

Herbae perennes foliis amplis; floribus 6 in verticillastris, bracteis caducis subtentis, glomerulis in spicis interruptis dispositis; calycibus ample pedicellatis in maturitate marcidis palealibus labiis acuminatis, labia superiore 5-venis; corollarum ut videtur vinacearum tubo cylindrato, ad basim intus papillis binis ornato, labia inferiore superiorem subaequante; staminibus e labia 3–4 mm. exsertis; styli glabri ramo postico longiore. Species typica est *S. palealis*.

This section would be sought in the key to the Sections near 38. *Iodophyllae*. However the key (p. 6) should be amended to read as follows:

F. Bracteae perstatae; calyces extus pilis longioribus extensis glandulosis viscidi 27. *Phoeniceae*. FF. Bracteae deciduae. G. Stamina ad tubi medium et infra posita 36. *Flexuosae*. GG. Stamina ad fauces posita. H. Styli glabri; corollarum labia inferior superiorem subaequans vel brevior I Flores oppositi in racemis dispositi; plantae glabrae orizabenses *38. Iodophyllae*. II Flores 6 in verticillastris in spicis interruptis dispositi; plantae sparse villosae guerrerenses *38a Pedicellata*. HH. Styli pilosi; corollarum labia inferior quam superior fere duplo longior *63b. Hintoniana*.

The habit of the plant is more suggestive of sect. *Carneae*, the shape of the corolla not unlike that of sect. *Sulcatae*. However, the fourth and fifth veins in the upper lip are fairly developed and the style is glabrous. The corolla is more slender than and of a different conformation from that of *Iodophyllae* and the flowers are distinctly verticillate.

175b. **Salvia palealis** Epling, sp. nov. (*Pedicellata*.) Herba perennis altitudine 1 m. caulibus superne pilis longioribus crassioribus sparse villosis et inter flores brevibus extensis glandulosis obsitis; foliorum laminis ovato-cordatis 11–13 cm. longis 6–9 cm. latis, in apice breviter acuminatis in basi cordatis petiolis villosis 6–7 cm. longis elatis, marginibus crenato-serratis, paginis ambabus sparse villosis; floribus 6 in verticillastris bracteis caducis subtentis in spicis interruptis 20–30 cm. longis dispositis glomerulis inter se 2–3 cm. distantibus; calycibus florentibus 11 mm. longis extus pilis brevibus capitato-glandulosis et crassioribus conspersis, labiis 4 mm. longis in maturitate calycibus mox palealibus et corollis marcidis adhaerentibus; corollarum tubo 19 mm. longo, labia superiore 5.5 mm. alta, inferiore subaequilonga; staminibus e labia 3–4 mm. exserta.

MEXICO. Guerrero: Montes de Oca, San Antonio, on rock in arroyo, *Hinton 14040* (type, Univ. Calif., L. A.).

179. S. LASIOCEPHALA H. & A. MEXICO. Michoacan: Coalcoman, Puerto Zarzamora, 1800 m., *Hinton 12715;* Huizontla, 440 m., *Hinton 12648;* Coalcoman, 1100 m., *Hinton 12330;* Apatzingan, Aguililla, 900 m., *Hinton 15296.*

180. S. GALINSOGIFOLIA Fern. MEXICO. Michoacan: Zitacuaro-Tuzantla, 800 m., *Hinton 13292* (if not this, then a glabrate form of the preceding).

182a. **Salvia compsostachys** Epling, sp. nov. (*Membranaceae*.) Herba perennis altitudine 30–50 cm., caulibus magnam partem simplicibus utrimque pilis subappressis molliter hirtellis internodiis quam folia brevioribus; foliorum laminis ovatis 5–8 cm. longis, 3–7 cm. latis, in apice acuminatis, in basi rotundatis, marginibus crenato-serratis, pagina superiore sparse hirtella, inferiore

praesertim ad venas sparse hirtella; petiolis 3–6 cm. longis; floribus plerumque 6 in verticillastris bracteis cyaneis reniformibus glabris 7–9 mm. longis in apice abrupte deltoideo-acuminatis subtentis, glomerulis inter se 1–2 cm. distantibus in spicas graciles corollis exclusis circiter 1.5 cm. latis 5–10 cm. longis dispositis; calycibus florentibus 5–6 mm. longis, extus pilis tenuibus extensis ut videtur subglandulosis sparse conspersis, in maturitate cyaneis vix longioribus tamen latioribus companulatis dentibus late deltoideis obtusis 2–2.5 mm. longis; corollarum tubo 4 mm. longo, labia superiore 2.5 mm. alta.

MEXICO. Nuevo Leon: Trail between Potrero Redondo and Las Ajuntas, Mun. de Villa Santiago, *C. H. Muller 2982* (type, Univ. Calif., L. A.). Horsetail Falls near Santa Catalina, *L. A. Kenoyer 342*. Very similar in aspect to *S. glabra* M. & G. which is known from Oaxaca from a single inadequate collection. It may be distinguished from that species by the smaller flowers and obtuse calyx teeth, as well as the pubescence. A pretty plant which might well repay cultivation.

189. **S. Mocinoi** Benth. MEXICO. Michoacan: Zitacuaro-La Campana, 2100 m., *Hinton 13520*. Abundantly collected in Guatemala by *Standley*.

190. **S. rubiginosa** Benth. GUATEMALA. Quiche: Nebaj, 6000 ft., *Skutch 1728*. Apparently this, the bracts rather small and the leaves nearly sessile but attenuate at the base.

200a. **Salvia curticalyx** Epling, sp. nov. (*Flocculosae*.) Herba perennis suffruticosa altitudine .5 m. frequenter tamen procumbens ramulis superne pilis ramosis sparse floccosis, infime fere glabris vel ut videtur pilis simplicibus sparse conspersis, internodiis sat elongatis; foliorum laminis late ovatis mediis 2.5–4.5 cm. longis, 1.5–4 cm. latis, in apice breviter acuminatis, in basi modo rotundatis modo truncatis, marginibus serratis sat convexis, paginis superioribus fere glabris et pilis subsimplicibus conspersis, inferioribus pilis ramosis sparse floccosis interdum fere glabris pallidioribus, petiolis mediis ad 2 cm. longis elatis; floribus 8 in verticillastris in spicas modo compactas, modo interruptas dispositis, bracteis caducis subtentis; calycibus florentibus 5 mm. longis, in maturitate paulo auctis extus densissime floccoso-lanatis, ore truncato, labiis vix 1 mm. longis superiore 7-venis; corollarum tubo 6 mm. longo, galea 5 mm. alta, labia inferiore 6 mm. longa; staminum connectivo 5.5 mm. longo; stylo utrimque piloso.

ECUADOR. Loja: Chinche, between San Pedro and Zaruma, *Penland and Summers 1191* (type, Univ. Calif., L. A.).

It is remarkable that this species has not heretofore been collected, for the region in which it grows is one of the best known in Ecuador, but like so many species of *Salvia* it may very well be a highly localized form. It is closely similar both to *Salvia cedrosensis*, endemic to Cedros Island and to *S. Cruikshanksii* which is evidently restricted to the province of Lima, Peru. It is distinguishable from both in the truncate nature of the

calyx as well as the dense floccose pubescence of that organ. In leaf habit, it is very similar to the latter, having mostly ovate leaves rounded at the base, soon glabrate, and borne on petioles 3–4 mm. long. A single detached branch, however, has larger broadly ovate leaves, truncate at the base, of different aspect and with petioles as long as 2 cm., in which respect it more nearly resembles *S. cedrosensis*. It seems improbable, however, that two distinct forms are represented; it is more likely that this branch is a more vigorous shoot. *S. loxensis*, known only from a collection made by Hartweg near Loja, is similar in many ways. Indeed, the section *Malacophyllae* is distinguishable from the section *Flocculosae* chiefly in habit and the simple pubescence. One is led to wonder whether *S. loxensis* is a glabrate form of the species now proposed. The calyces of the former are not so markedly truncate, nor is there any evidence of branching hairs, and in comparing Hartweg's plant it seems probably distinct.

204. S. LYCIOIDES Gray. MEXICO. Coahuila: Sierra de la Madera, Cañon de Agua, Mun. de Cuatro Cienegas, *C. H. Muller 3219*.

214a. **S. capillosa** Epling, sp. nov. (*Scorodonia*.) Suffrutex altitudine ad 1.5 m. ramis superne et inter flores pilis decurvis et setis ad 3 mm. longis subglandulosis valde setosis; foliorum laminis cordatis, 6–8 cm. longis, 3.5–4 cm. latis, in apice acutis, petiolis 1.5–2.5 cm. longis elatis, marginibus crenato-serratis, paginis ambabus molliter pubescentibus superiore viride inferiore cinerea; floribus 3–6 in verticillastris bracteis deciduis subtentis, glomerulis inter se 1–2 cm. distantibus in spicis interruptis dispositis; calycibus florentibus 7 mm. longis extus pilis eis ramulorum similibus setosis; corollarum pallide caerulearum tubo 7 mm. longo, intus nudo, labia superiore, 4.5 mm. alta

MEXICO. Michoacan: Zitacuaro-Loma Larga, *Hinton 13020*. (Type, Univ. Calif., L. A.). In following the key to the section *Scorodonia* (p. 167) this species would probably be sought near *S. pannosa* or *S. Keerlii*. However, the key is based upon the alternative either of decurved eglandular hairs on the stem or of spreading glandular ones. In *S. capillosa* both types are present and while the longer ones may be eglandular they are more commonly glandular. However, the species is well marked by the unusually long spreading hairs and suggests *S. Urica* in habit.

225. S. URICA Epling. GUATEMALA. Quiche: Chichicastenango, 1850–2100 m., *Standley 62366*.

239. S. AMISSA Epling. Fish Creek Canyon, Maricopa Co., *Kearney and Peebles 14480; Epling and Pratt*. Previously known only from the type, collected in 1881 by Pringle in the Santa Catalina Mts. So similar to *S. pallida* of Argentina is this species, that, if found amongst a collection of Argentina plants it might readily be mistaken for that. At the same time, it is like *S. similis* of Baja California. It differs from the former particularly in the ample paniculate inflorescence, the somewhat smaller

flowers and the proportionately and actually longer leaves with smaller indentations. In pubescence it is about the same. From *S. similis* it differs chiefly in the larger and proportionately narrower leaves and especially in the conformation of the calyx and the nature of the pubescence. The calyx lobes of *S. similis* are notably shorter and the pubescence is much finer and denser. In Fish Creek Canyon it is abundant in the sandy bottom amongst boulders, growing in the shade of *Platanus, Juglans, Fraxinus* and *Populus*. The associated shrubs are chiefly those of the *Larrea* formation.

239a. **S. pseudopallida** Epling, sp. nov. (*Farinaceae.*) Herba perennis altitudine ad 60 cm. caulibus utrimque pilis crispis sparse pubescentibus; foliorum laminis ovatis 6–7 mm. longis, 3–4 mm. latis supra medium acuminatis, in basi rotundatis, margine serrata, pagina superiore sparse hirtella, viride, inferiore pallidiore molliter pubescente; petiolis gracilibus 3–4 cm. longis; floribus 3–6 in verticillastris bracteis caducis subtentis, glomerulis inter se 1–2.5 cm. distantibus, in spicas nullomodo paniculatas sat confertas approximatis; calycibus florentibus 7–8 mm. longis, extus molliter hirtellis, labia superiore 5-venis; corollarum caerulearum tubo circiter 10 mm. longo, labia superiore 6 mm. alta.

MEXICO. Coahuila: Sierra de la Madera, Cañon del Agua, Mun. de Cuatro Cienegas, *C. H. Muller 3226* (type, Univ. Calif., L. A.). Similar in some respects to *S. amissa*, in other respects to *S. pallida*, but with broader leaves than either. In the general key it might be sought under *41. Flocculosae* (p. 13) rather than *46. Farinaceae*.

240. **S. SIMILIS** Bdge. MEXICO. Baja California: Los Angeles, *Whitehead 671*. 41 mi. S. of Pozo Aleman, *Shreve 7020*. 18 mi. north of San Ignacio, *Wiggins 7892*. 36 mi. S. of Pozo Aleman, *Wiggins 7882*. Purissima, *Gentry 4222*.

242. **S. FARINACEA** Benth. MEXICO. Coahuila: Sierra de la Madera, Cañon del Pajarito, Mun. de Cuatro Cienegas, *C. H. Muller 3167*.

243a. **S. Jacobi** Epling, sp. nov. (*Farinaceae.*) Herba perennis bella altitudine 1.5 m., caulibus utrimque pilis minutis appressis cinereis internodiis sat elongatis; foliorum laminis lanceolatis 4–5 cm. longis, acuminatis, in basi rotundato-angustatis, margine serrata, pagina superiore viride glabra, inferiore pilis minutissimis appressis incanis, petiolis vix 1 cm. longis elatis; floribus 6 et ultra in verticillastris bracteis caducis subtentis, glomerulis inter se .5–1 cm. distantibus in spicas sat confertas approximatis; calycibus florentibus 3.5–4 mm. longis, extus pilis minutis appressis cinereis subfarinaceis tamen purpureis, in maturitate paulo auctis ore breve subtruncato, labia superiore 3-venis; corollarum caerulearum tubo 6 mm. longo, labia superiore 3.5 mm. alta.

MEXICO, Guerrero: Mina, near Laguna, *Hinton 14110* (type, Univ. Calif., L. A.). This species seems clearly to be allied to *S. farinacea* and

would be sought there in the general Key. However, in the sectional Key its position is ambiguous. Additional material of *S. amissa* and *S. similis* shows also that the bracts of the former are soon deciduous and of the latter sometimes tardily deciduous. The sectional Key (p. 186) may therefore be rearranged to read as follows:

Petioli saepius 1–4 cm. longi
  Plantae Argentinae .... 241. *S. pallida*
  Plantae boreali-americanae
    Calycum labiae 3–5 mm. longae in maturitate
    amplae hiantes habitus *S. ballotaeflorae* .... 238. *S. platycheila*
    Calycum labiae vix 3 mm. longi nullomodo hiantes,
    ore breve frequenter subtruncato
      Plantae Californiae inferioris bracteis subper-
      statis, foliis juvenilibus subtus minute et dense
      incana in maturitate glabrata.............. 240. *S. similis*
      Plantae continentis bracteis caducis, foliis con-
      coloribus (vide tamen *S. Jacobi*) glabratis vel
      subtus molliter pubescentibus
        Calyces extus dense et molliter appresso-
        hirtelli; plantae praesertim Texanae foliis
        glabratis .... 242. *S. farinacea*
        Calyces extus pilis crispis plus minusve
        extensis etiam lanulosis hirtelli; foliis subtus
        molliter pubescentibus vel glabratis
          Calyces florentes 4.5 mm. longi extus lanu-
          lati; plantae coahuilenses.............. 243. *S. lanicalyx*
          Calyces florentes 6–8 mm. longi, crispo-
          hirtelli vix tamen lanulosi
            Plantae arizonicae corollorum tubis
            6.5–7 mm. longis................... 239. *S. amissa*

            Plantae coahuilenses corollarum tubis
            10 mm. longis..................... 239a. *S. pseudopallida*
Petioli saepius minusquam 1 cm. longi
  Calyces extus molliter appresso-hirtelli; folia subtus
  discoloria minute incana; plantae Guerrero (vide
  etiam *S. farinaceam*)......................... 243a. *S. Jacobi*
  Calyces extus pilis plus minusve extensis vix appres-
  sis; folia concoloria saepius glabrata
    Herbae variae a Carolina usque ad Texas et in
    Nuevo Leon incolunt...................... 244. *S. azurea*
    Herbae imprimis mexicanae in Texas solum in
    parte ad Chihuahua spectante incolunt
      Caules superne pilis brevibus extensis glandu-
      losis induti; radices tuberiferae; folia ellip-
      tica .... 247. *S. oblongifolia*

Caules pilis extensis saepius longioribus setosi
nisi omnino glabri; folia linearia
　　Pili acuti eglandulosi.................... 245. *S. leptophylla*
　　Pili capitato-glandulosi.................. 246. *S. heterotricha*

245. S. LEPTOPHYLLA Benth. var. GLABRA (Gray) Epling. MEXICO. Chihuahua: Between Mesteñas and Ojinaga near Cruces, *I. M. Johnston 7974.*

268. S. KELLERMANII J. D. Smith (see under 351).

273. S. SACCULUS Epling. MEXICO. Nuevo Leon: Alaman, 15 mi. S. W. of Galeana, *Mueller and Mueller 1133; M. Taylor 218.* (In early flower only, but apparently this.)

274. S. CONNIVENS Epling. MEXICO. Hidalgo: Jacala, *O. E. White; M. T. Edwards 796; L. A. Kenoyer 631.*　　　　　　　　　　　·

278. S. POLYSTACHYA Ort. What is apparently an albino race of this species has been collected at several places in Michoacan by Hinton in the regions of Zitacuaro and Coalcoman (*13379; 13343; 12535; 12533; 12532; 12660*).

279. S. COMPACTA Kuntze. PANAMA. Chiriqui: Rio Chiriqui Viejo Valley near El Volcan, *P. White 208.* Apparently the same species but with corolla tubes 8 mm. long, Chiriqui: trail from Paso Ancho to Monte Lirio, upper valley of Rio Chiriqui Viejo, *P. H. Allen 1590.*

282. S. PLURISPICATA Epling. MEXICO. Michoacan: Zitacuaro-Las Canoas, *Hinton 13549.*　　　　　　　　　　　　　·

293. S. PSEUDOGRACILIS Epling. Conspecific with 319 *S. myriantha* Epl., which see.

294. S. GRACILIS Benth. MEXICO. Michoacan: Zitacuaro-Cerro Pelon, 3200 m., *Hinton 13233;* 35 m. east of Morelia, 7000 ft., *Rowntree 264.* Morelos: Valle del Tepeite, *Lyonnet.* Guerrero: Galeana, Piedra Ancha, *Hinton 14225;* Pie de la Cuesta-Toro Muerto, 2840 m. (*Hinton 11226*). This specimen has flowers with the corolla tube full 10 mm. long, in this respect like *S. purpurascens* M. & G., the extreme for this species. Like the type of *S. purpurascens* it has broader less acuminate leaves. Mina, Teotepec, *Hinton 14297;* Laguna, *Hinton 14113;* Puerto Rico, *Hinton 14161.* GUATEMALA. Quezaltenango: between Fuentes Georginas and Zunil, *Standley 67330;* Palestina, *Standley 66347.* Tontonicapan: Desconsuelo, *Standley 62732;* Cumbre del Aire, *Standley 65895.*

295. S. MEMBRANACEA Benth. MEXICO. Chiapas: Volcan de Tacana, Chiquihuite, 2800 m., *Matuda 2843.*

295a. S. IRAZUENSIS Fern. PANAMA. El Potrero Camp, Chiriqui Volcano, 2800–3000 m., *Pittier 3105.* Boquete, Bajo Chorro, Chiriqui, 6000 ft., *M. E. Davidson 81.* Loma Larga to Summit, Volcano Chiriqui, *Woodson, Allen, and Seibert 1037.* Previously referred by me to *S. membranacea*

Benth., from which it may be distinguished chiefly by the small fine even hairs of the inflorescence which are partly glandular, but not coarse as in that species. Other Costa Rican specimens are probably referable here. I have compared the Panama specimens with Fernald's type. *S. irazuensis* is distinguishable from *S. debilis* of northern Colombia chiefly by the glabrous calyces and stems of that species.

296. S. IODOCHROA Fern. Apparently this, collected by P. H. Allen (*No. 1442*) in PANAMA. Chiriqui: trail from Cerro Punta to headwaters of Rio Caldera.

296a. **Salvia punicans** Epling, sp. nov. Herba perennis vel suffrutex altitudine ad 1.5 m. caulibus superne praesertim inter flores pilis minutis glandulosis dense obsitis et paucis crassis longioribus conspersis; foliorum laminis pulchre cordato-ovatis 8–12 cm. longis, 5–10 cm. latis, in apice acuminatis, in basi cordatis petiolis 5–8 cm. longis elatis, pagina superiore fere glabra, inferiore ad venas pilis minutis glandulosis dense obsita; floribus 6 in verticillastris in spicis interruptis 10–15 cm. longis dispositis glomerulis inter se 1.5–2.5 cm. distantibus; calycibus florentibus 11 mm. longis, extus pilis minutis glandulosis dense obsitis et crassis eglandulosis sparsissime conspersis, labia superiore interdum sub-5-venis; corollarum punicearum tubo 20 mm. longo, labia superiore 8.5 mm. longa, inferiore paulo longiore.

MEXICO. Guerrero: Galeana, inter Pie de la Cuesta et Toro Muerto, 2840 m., in pineto-quercetis, *Hinton 11225; 11224* (type, Univ. Calif., L. A.).

Following is an amended key to the section *Carneae* (p. 228); because of the paucity of material for most of the species, it is still far from satisfactory (see 293 *S. pseudogracilis*):

Corollarum tubi 7–10 mm. longi
    Caules inter flores pilis articulatis purpureis saepius
    villosuli; folia in basi saepius subcordata; plantae
    Colombianae et Venezuelanae................... 298. *S. carnea*
    Caules inter flores pilis minutis capitato-glandulosis
    obsiti; folia in basi rotundata vix cordata; plantae
    mexicanae et guatemalenses................... 294. *S. gracilis*
Corollarum tubi 10–20 mm. longi
    Corollarum tubi 20 mm. longi; foliorum venae subtus
    pilis minutis capitatis glandulosae; plantae guerre-
    renses .... 296a. *S. punicans*
    Corollarum tubi 10–16 mm. longi
        Corollarum labia superior 7.5–9 mm. alta
            Plantae colombianae foliis glabris in basi rotun-
            datis .... 299. *S. debilis*
            Plantae mexicanae vel costaricenses
                Folia pulchre cordata, villosa; Costa Rica... 296. *S. iodochroa*

Folia in basi rotundata utrimque glabra;
Hidalgo .... 297. *S. simulans*

Corollarum labia superior 4.5–7 mm. alta

Caules inter flores pilis crassiuculis articu-
latis plus minusve ornati; folia iu basi plus
minusve cordata .

Plantae colombianae................... 300. *S. Killipiana*

Plantae mexicanae.................... 295. *S. membranacea*

Caules inter flores pilis gracilioribus brevi-
oribus ornati

Plantae chiapenses; folia glabra in basi
rotundato-angustata .... 297a. *S. ionocalyx*

Plantae costaricenses etiam panamenses
foliis in basi plus minusve cordatis et sub-
tus ad venas plus minusve pilis crassius-
culis ornatis .... 295a. *S. irazuensis*

310. S. ROSCIDA Fern. MEXICO. Sonora: Curahui, Rio Mayo, *Gentry 3651*. Apparently this species but the leaves hirtellous on the veins beneath with rather coarse hairs and the bracts 3–4 mm. long and mostly per-sistent.

312a. **Salvia cyanantha** Epling, sp. nov. (*Angulatae.*) Herba perennis gracilis verisimiliter suffruticosa internodiis sat elongatis glabratis, solum in sulcis appresso-hirtellis nisi inter flores pilis brevibus extensis violaceis puberu-lis; foliorum laminis 5–6 cm. longis, pulchre acuminato-ovatis, in basi rotun-datis, marginibus serratis, paginis ambabus sparse hirtis, petiolis gracilibus circiter 2 cm. longis elatis; floribus saepius tribus in verticillastris bracteis caducis non visis subtentis, in spicis interruptis laxis gracilibus dispositis, glomerulis inter se 1–3 cm. distantibus; calycibus florentibus cyaneis 8–9 mm. longis, sat tenuibus extus pilis violaceis crassiusculis sparse villosis et minutis capitato-glandulosis conspersis, in maturitate 10–11 mm. longis pedicellis 3–4 mm. longis elatis; corollarum atro-cyanearum tubo arcuato-assurgente 15 mm. longo ad basim obscure constricto, labia superiore 4.5 mm. alta, infe-riore 6–8 mm. longa; stylo postice hirsuto.

MEXICO. Michoacan: Coalcoman, *Hinton 15350* (type, Univ. Calif., L. A.). The plant suggests *S. gracilis* with dark blue flowers and evidently falls somewhere near *S. arthrocoma*.

314a. S. LANGUIDULA Epling. MEXICO. Guerrero: Montes de Oca, San Antonio-Buenos Aires, *Hinton 14061*; Capirial, *Hinton 13010*. Appar-ently this but the calyces glabrous. Another specimen, collected in Michoa-can, Coalcoman, *Hinton 12598*, is scarcely separable from these. Still another, collected in Guerrero, Galeana, Tecpan-El Verde, *Hinton 14338*, is similar, but has the leaf habit more suggestive of *S. Seemannii* as it occurs in Sonora.

Because of the rather coarse nature of the pubescence of the type specimen of *S. languidula*, a relationship with *S. fusca* seemed probable. This species occurs in Guerrero and is known from a single, none too ample specimen (*Langlassé 216*). The specimens mentioned above, particularly those from Montes de Oca, are very like the type of *S. languidula* but are almost glabrous. A few minute decurved hairs may be seen on the pedicels and along the branchlets. In this respect they are like *S. albiflora* but do not have the elongate and rather strict inflorescence of that species. A specimen collected by *Mexia* (*No. 8729*) in Guerrero, distr. Adama, and previously referred by me to *S. longispicata*, has the pubescence and coarser habit of that species, but is hardly typical of that species as it occurs in Jalisco and Michoacan.

319. S. MYRIANTHA Epling. *S. pseudogracilis* Epling in Rep. Spec. Nov., Beih. 110: 229. 1939. GUATEMALA. Quezaltenango: Cumbre de Tuilacan, near San Martin Chile Verde, *Standley 67771; 67813;* Fuentes Georginas, Volcan de Zunil, *Standley 67474;* Aguas Amargas, Volcan Zunil, *Standley 65337.* Scarcely separable from these specimens save for the villous pubescence of strict jointed hairs are the following; pubescence of the same order occurs on the vegetative branchlets of the above-named specimens, but the flowers of that group are pale purple, those of the following white: GUATEMALA. San Marcos: Rio San Ramon, *Standley 66184;* El Boqueron, *Standley 66298.* Huehuetenango: San Juan Atitlan, *Skutch 1156* (cordate leaves). This second form would not be readily found in the sectional key because of the longer hairs on the calyces. It might be sought near *S. roscida* or *S. arthrocoma*.

319a. S. psilophylla Epling, sp. nov. (*Angulatae.*) Herba perennis altitudine ad 2 m. caulibus superne pilis brevibus densis extensis molliter hirtellis; foliorum laminis ut videtur flaccidis membranaceis ovatis 12–14 cm. longis, 6–8 cm. latis, in apice acuminatis, in basi rotundatis, marginibus serrulatis, paginis ambabus glabris nisi ad venas sparsissime hirtellis, petiolis 7–8 cm. longis elatis; floribus 3–6 in verticillastris bracteis membranaceis ovato-attenuatis 6 mm. longis caducis subtentis, glomerulis inter se 1–2 cm. distantibus, in spicis interruptis ut videtur laxis 20–25 cm. longis dispositis; calycibus florentibus 9 mm. longis tenuibus extus ad venas hirtellis, in maturitate paulo auctis et pedicellis 6–9 mm. longis elatis; corollarum rosearum vel pallide caerulearum tubo 10 mm. longo, labia superiore 5.5 mm. alta; staminum connectivo 6.5 mm. longo.

PANAMA. Chiriqui: Rain forest at Bajo Chorro, Boquete district, 6000 ft., *M. E. Davidson 60;* near New Switzerland, middle valley of Rio Chiriqui Viejo, 1800–2000 m., *P. H. Allen 1355* (type, Univ. Calif., L. A.). This species would probably be sought in the sectional key near *S. myriantha*.

331. S. ALBIFLORA M. & G. MEXICO. Michoacan: Zitacuaro-San José Purua, *Hinton 13054.*

335. S. FLUVIATILIS Fern. MEXICO. Michoacan: Zitacuaro-Angangueo, 2090 m., *Hinton 11897;* Coalcoman, Chacalapa, 2000 m., *Hinton 13774.* Very similar to *S. xalapensis* of the Cordoban region, and scarcely separable. That species is most readily distinguished by the coarser more spreading but curled hairs in the inflorescence, while in *S. fluviatilis* the hairs are finer and curl downward.

337. S. DYMOCHARIS Epling. COSTA RICA. San José, El General, 1525 m., *Skutch 4187.* Apparently this but the corolla tube about 15 mm. long.

338. S. ALVAJACA Oerst. *S. inaequilatera* Cufodonti, described from Mt. Irazu, Costa Rica. GUATEMALA. Quezaltenango: Slopes of Volcan de Zunil, Aguas Amargas, *Standley 65444;* Finca Pireneos, Santa Maria de Jesus, *Standley 68299.* PANAMA. Chiriqui, Chiriqui Viejo Valley, *G. White 99; P. White 167.*

347a. S. CHIAPENSIS Fern. GUATEMALA. Huehuetenango: South slope of Sierra Cuchumatanes above Chiantla, 10,300 ft., *Skutch 1275.* Apparently this.

351. S. KELLERMANII J. D. Smith. *S. Maxonii* Epling in Rep. Spec. Nov., Beih. 110: 266. 1939. GUATEMALA. Quezaltenango: Santa Maria de Jesus, *Standley 67196;* Escuintla Palin, *J. R. Johnston 1194;* Palin, *Standley 60113.*

353a. **Salvia synodonta** Epling, sp. nov. (*Briquetia.*) Herba perennis altitudine ad 1.5 m., caulibus utrimque glabra nisi in sulcis obscurissime appresso-hirtellis; foliorum laminis ovatis sat tenuibus 6–9 cm. longis, 5–7 cm. latis, in apice acuminatis, in basi rotundatis vel rotundato-angustatis, utrimque nisi ad venas obscure hirtellis glabris, margine serrata, petiolis gracilibus 2–3.5 cm. longis elatis; floribus 1–3 in verticillastris bracteis perstatis lanceolatis 3–4 mm. longis subtentis, in spicis sat confertis dispositis, glomerulis inter se .5–1 cm. distantibus; calycibus florentibus 8–9 mm. longis glaberrimis, labiis deltoideis 2.5 mm. longis, inferioris dentibus connatis, pedicellis minutissime retrorso-hirtellis 2.5–3 mm. longis elatis; corollarum atro-caerulearum tubo 11–12 mm. longo, labia superiore 6.5–7.5 mm. alta, inferiore breviore.

MEXICO. Michoacan: Huizontla near Coalcoman, *Hinton 12649; 12576* (type, Univ. Calif., L. A.). Very similar to the type of *S. umbratilis* Fern. collected by Langlassé at an undesignated station in this general region, either in Michoacan or Guerrero. It differs, however, in the narrower, longer bracts, in the smaller flowers, in the connate lower calyx teeth and in the nature of the pubescence where this is perceptible. *S. umbratilis,* although almost glabrous, nevertheless is hirtellus in the inflorescence with small spreading or ascendent hairs. The pedicels of *S. synodonta*

bear minute retrorse hairs. The key (p. 268) may be amended to read as follows:

> Herbae mexicanae; corollarum tubi 11–15 mm. longi
>> Pedicelli pilis minutis retrorsis hirtelli; calycum dentes
>> inferiores connati; corollarum tubi 11–12 mm. longi. .   **353a.** *S. synodonta*
>> Pedicelli pilis minutis ascendentibus hirtelli; calycum
>> dentes inferiores liberi acuminati; corollarum tubi
>> 15 mm. longi. . . . .   **353.**   *S. umbratilis*
> Herbae Ind. Occ. etc. etc.

354. S. MEXICANA L. MEXICO. Sonora: Pinal in Sierra Charuco, among oaks and pines, *Gentry 1702.* Hidalgo: Jacala, *L. A. Kenoyer.*

354a. S. ATROPAENULATA Epling. MEXICO. Guerrero: Mina, Toro Muerto-Campo Morado, 1800 m., *Hinton 11239.* Michoacan: Zitacuaro-Cerro Pelon, 3200 m., *Hinton 13234;* edge of pine woods on road from Toluca to Zitacuaro, *Rowntree 174.* The type, *Mexia 9056, Hinton 13234,* and *Rowntree 174,* have corolla tubes 14–15 mm. long. *Hinton 11239* has corolla tubes as much as 23 mm. long. The plants are otherwise very similar and characterized by the glandular as well as eglandular types of pubescence.

362. S. DICHLAMYS Epling. MEXICO. Guerrero, Aguazarca, in pine forest, *Hinton 10450.* Michoacan, Zitacuaro, toward Laureles, *Hinton 13001.* Zitacuaro, toward Bosque, *Hinton 11940.* Zitacuaro toward San Cristobal, *Hinton 11988.* This species has the habit and pubescence which strongly suggest 363a *S. nigriflora.* The corolla is a deep wine red rather than the bright carmine distinctive of the section. However, the conformation of the corolla is fairly typical. In other words, *S. dichlamys* has characteristics of section *Fulgentes* and of section *Nigriflorae* and stands in an intermediate position.

363. S. MICROPHYLLA Kunth. MEXICO. Chiapas: Near Zempoala Lakes, 9000 ft. Mt. Tacana, *Matuda 2478.* Var. NEUREPIA (Fern.) Epling. Hidalgo. Jacala, *Kenoyer 630.*

63a. SECTION NIGRIFLORAE

Herbae perennes vel suffrutices verisimiliter e caudice lignoso; foliis oblongis sat parvis coriaceis valde bullatis subsessilibus; floribus oppositis bracteis caducis subtentis in racemis paucifloribus laxis dispositis; calycum labia superiore 5-venis; corollarum atro-cyanearum tubo sat amplo ad basim plus minusve invaginato et intus papillis binis ornato, labia superiore galeata, inferiore quam superior duplo longiore deflexa; staminibus ad fauces positis, connectivo ad medium dente acuto extenso ornato; styli hirsuti ramo postico longiore. Species typica est *S nigriflora.*

363a. **Salvia nigriflora** Epling, sp. nov. (*Nigriflorae.*) Herba perennis altitudine .5 m. caulibus superne et inter flores pilis longioribus extensis graci-

libus plus minusve glandulosis pilosis; foliorum laminis 5.5–8 cm. longis, 12–22 mm. latis, oblongis, in apice obtusis, in basi rotundatis, petiolis 2–3 mm. longis elatis, pagina superiore glabra subnitida valde bullata, inferiore albotomentella, venulosa et ad venas pilis longioribus sparse ornata, marginibus crenulatis; floribus paucis oppositis in racemis laxis circiter 10 cm. longis, glomerulis inter se 1–5 cm.; calycibus florentibus 6–10 mm. longis, extus sparse pilosis vix tamen glandulosis; corollarum atro-cyanearum tubo amplo 12 mm. longo, labia superiore 9 mm. alta, inferiore 13 mm. longa; staminum connectivo 13–14 mm. longo.

MEXICO. Michoacan: Coalcoman, Ocorla, 1700 m., *Hinton 13787;* Sierra Naranjillo, 1300 m., *Hinton 13956* (type, Univ. Calif., L. A.); Sierra Torricillas, 2400 m., *Hinton 12410.* The deep blue color, the singular habit (save for *362 S. dichlamys* of which see above) and the differences in conformation of the lower lip of the corolla, all suggest segregation of this species as a monotypic section. In the key to the sections it would probably be sought (p. 12) near *46. Farinaceae,* by reason of the oblong or elliptical leaves. It may be readily distinguished, however, by its corrugated leaves, by the dense tomentum on the lower surface and by the opposite flowers which are dark blue.

63b. SECTION HINTONIANA

Frutices vel suffrutices habitus sectionis Fulgentium foliis sat amplis; floribus 3 in verticillastris bracteis caducis subtentis in spicis approximatis; calycum labia superiore 5-venis; corollarum pulchre coccinearum tubo ad basim subinvaginato et intus rugis binis vel papillis brevibus ornato, labia superiore tubum aequante, inferiore amplissima furcata quam superior fere duplo longiore; staminibus e labia superiore 3–4 mm. exserta; styli pilosi ramo postico longiore. Species typica est *S. praestans.*

This section would be sought in the key probably near *36. Flexuosae* or *38. Iodophyllae.* The amended key may be seen under *38a. Sect. Pedicellata.*

363b. **Salvia praestans** Epling, sp. nov. (*Hintoniana.*) Suffrutex altitudine ad 2 m. ramulis pilis decurvis pubescentibus et longioribus plus minusve glandulosis ad 2.5 mm. longis setaceis; foliorum superiorum laminis 10–12 cm. longis, 5 cm. latis ovato-lanceolatis, in apice acutis vel longe acuminatis, in basi rotundato-truncatis, petiolis 1.5 cm. longis elatis, marginibus serratis, pagina superiore bullata viride pubescente, inferiore molliter cinereo-pubescente, supremis similibus sessilibus; floribus 3 in verticillastris bracteis setaceis caducis subtentis, glomerulis inter se 1.5 cm. distantibus, in spicis 12 cm. longis approximatis; calycibus florentibus 16–17 mm. longis, extus pilis mollibus pubescentibus et longioribus crassis glandulosis setaceis; corollarum tubo 18 mm. longo, ad basim subinvaginato et intus rugis binis vel papillis brevibus ornatis, labia

superiore tubum aequante, inferiore 28 mm. longa 20 mm. lata; staminibus e labia 3-4 mm. exsertis.

MEXICO. Guerrero: Mina, Toro Muerto, 2180 m., in oak and pine forest, *Hinton 11095* (type, Univ. Calif., L. A.).

381. S. SESSEI Benth. MEXICO. Michoacan: Coalcoman, Sierra Torricillas, 1800 m., *Hinton 12812;* Zitacuaro-Laurelles, 1400 m., *Hinton 13033.*

387. S. CARDINALIS Kunth. MEXICO. Michoacan: Zitacuaro-Cacique, 3250 m., *Hinton 13172.*

391. S. HOLWAYI Blake. COSTA RICA. San José, El General, 1430 m. GUATEMALA. Sacatepequez: Finca El Hato, Antigua, 1950–2040 m., *Standley 61145.* Baja Verapaz: Santa Rosa, 1650 m., *Standley 69894.* Quezaltenango: Palestina, 2700 m., *Standley 66325.* Chimaltenango: Patzicia, 1800 m., *Standley 58655;* Parramos, 1650–1800 m., *Standley 59887;* Volcan de Acatenango, Las Calderas, 2100–2400 m., *Standley 61800, 61793;* Patzum, 2100 m., *Standley 61482;* San Marcos, *J. R. Johnston 1230.* Quiché: Chichicastenango, 1830–1880 m., *Standley 62380.* San Marcos: Rio Tacana, San Antonio, *Standley 66148, 66084, 66110.* The degree of pubescence is quite variable. The leaves may be almost glabrous, or the lower surface may be almost tomentose with rather coarse hairs. The inflorescence usually bears both short capitate glands and longer stouter hairs. In some specimens the former may be suppressed, as in *Standley 59887.* In others the longer hairs may be mostly suppressed and the inflorescence quite viscid, as in *Johnston 1230.*

392. S. WAGNERIANA Polak. MEXICO. Chiapas: Volcan de Tacana, 2100 m., *Matuda 2972.*

394. S. PUBERULA Fern. MEXICO. Hidalgo: Jacala, *Kenoyer 775.* Nuevo Leon: La Trinidad-Potrero Redondo, Mun. de Villa Santigo, *C. H. Muller 2944.* The type collection of this species is characterized by spreading rather short glandular hairs. Pennell's specimen (*No. 17815*), probably gathered in the same region, has longer spreading jointed hairs abundant in the inflorescence; Muller's specimen is similar with leaves 13 cm. long. Kenoyer's specimen, cited above, has flowering calyces scarcely 13 mm. long and a corolla with tube 24 mm. long but pubescence similar to the type. The bracts are apparently always small and caducous. The key (p. 296) may therefore be modified to read:

Folia ad basim rotundata vel cordata; plantae mexicanae .... 393. *S. involucrata*
Verticillastra bracteis parvis inconspicuis caducis subtenta
Plantae guatemalenses foliis rarius omnino glabris petiolis saepius 1-4 cm. longis.................. 391. *S. Holwayi*

Plantae mexicanae foliis utrimque glabris petiolis
saepius 3–6 cm. longis........................ 394. *S. puberula*

398. S. SUBHASTATA Epling. MEXICO. Guerrero: Montes de Oca, San Antonio, *Hinton 11714, 11715*. Previously known only from the type which was of uncertain locality; the flowers of that (*Langlassé 570*) were said to be white and pink. Hinton's plants are assuredly conspecific. The bracts are showy purple, 2–3 cm. long, soon falling. The corolla is said by Hinton to be yellow; its tube is 27–30 mm. long. Shrubs 2 m. tall.

401a. **Salvia gravida** Epling, sp. nov. (*Skeptostachys.*) Herba perennis crassa altitudine ad 3 m. caulibus superne pilis crassis 2–2.5 mm. longis pilosis; foliorum laminis cordatis bullatis tenuibus longitudine ad 20 cm., petiolis ad 15 cm. longis elatis, in apice acuminatis paginis ambabus sparse villosis et inferiore ad venas minute glandulosa, marginibus crenato-serratis; floribus 6 in verticillastris bracteis amplis perstatis viridibus circumplicantibus subtentis, in spicis cylindratis densis 30 cm. longis et ultra 5–6 cm. diametro demum gravidis et pondere suo demissis; calycibus florentibus 24–26 mm. longis extus fere glabris sat tenuibus venulosis, in maturitate paulo auctis, pedicellis ad 15 mm. longitudine elatis; corollarum rubrarum tubo 30 mm. longo, labia superiore 18–21 mm. alta, inferiore paulo longiore; staminum connectivo 32–34 mm. longo.

MEXICO. Michoacan: Coalcoman, Sierra Torricillas, 2400–2680 m., *Hinton 12799; 12397; 12355* (type, Univ. Calif., L. A.). This species is apparently allied to *S. Regnelliana* of Brazil, which is very similar both in flower structure and in habit of inflorescence. I have accordingly referred it to section *Skeptostachys*. The general key to the sections is accordingly somewhat misleading inasmuch as *Skeptostachys* is referred to there as South American only. It is a beautiful plant and flowers during November and December in Los Angeles.

423. S. MARCI Epling. MEXICO. Baja California: Los Encinos and Arroyo Hondo, Sierra Giganta, *Gentry 4254, 4143*.

437. S. IODANTHA Fern. This species, common in Michoacan, is ordinarily characterized by a corolla which is a deep wine red. An albino form has recently been collected between Zitacuaro and Copandaro, 2600 m., *Hinton 13568*. A form with a pure rose pink corolla was collected near Coalcoman in the Sierra Torricillas, *Hinton 12797*. The latter recommends itself highly as a cultivated plant, no less than the typical form.

439. S. ARBUSCULA Fern. Known previously from the general region of the "Sierra Madre" in Guerrero. It has now been collected in Guerrero: Montes de Oca, San Antonio, Buenos Aires, *Hinton 11699*, and in Michoacan: Coalcoman, at Puerto Zarzamora, *Hinton 13729, 12921, 13722*.

442. S. PURPUREA Cav. HONDURAS. Yoro: Yoro, *J. B. Edwards 753*; Tegucigalpa, *Von Hagen 1243*.

450. S. LONGISTYLA Benth. MEXICO. Michoacan: 35 mi. west of Zitacuaro, 5500 ft., *Rowntree 273;* between Zitacuaro and Bosque, *Hinton 13434.*

451. S. NERVATA M. & G. GUATEMALA. Totonicapan: Cumbre del Aire, *Standley 62655, 65900.* Quezaltenango: Palestina, 2700 m., *Standley 66362;* Volcan Santa Maria, Palojunaj, 2400–3768 m., *Standley 67596, 67606, 67654, 67588, 67650;* Santa Maria de Jesus, 1650 m., *Standley 67250.* San Marcos: Barranco Eminencio, 2700 m., *Standley 68499;* El Boqueron, 2700 m., *Standley 66279.*

453. S. CURTIFLORA Epling. GUATEMALA. San Marcos: San Antonio along Rio Tacana, 2460 m., *Standley 66136, 66149, 66172.* Dept. Chimaltenango: Las Calderas, 1800–2100 m., *Standley 60059, 60031, 61955.* Dept. Quezaltenango: Fuentes Georginas to Zunil, 2500 m., *Standley 67337, 67412, ? 67335;* Palestina, 2700 m., *Standley 66335;* Cumbre de Tuilacan, San Martin Chile Verde, 2400 m., *Standley 67779, 67766, 67778.*

454. S. EXCELSA Benth. MEXICO. East of Orizaba, 6500 ft., *Rowntree 111.* This species was ascribed to Guatemala by Bentham and has not since been collected until found by Miss Rowntree. After examination of her specimen and comparison with the type of *S. venosa* Fern., described from Chiapas, I am convinced that they are conspecific and that *S. venosa* is also conspecific with *S. excelsa.* That species was described from cultivated plants which were grown from presumed Guatemalan seeds.

467a. Salvia unguella Epling, sp. nov. (*Secundae.*) Suffrutex glabra, altitudine ad 1 m., caulibus superne nisi pilis minutissimis glabris, internodiis petiolos subaequantibus; foliorum laminis ovato-ellipticis 10–15 cm. longis, 6–8 cm. latis, in apice caudato-acuminatis, infra medium angustatis etiam ad petiolos 2–8 cm. longos leniter acuminatis, utrimque glabris, marginibus serratis; floribus 3–6 et ultra in verticillastris inter se .5–1.5 cm. distantibus in spicas 7–15 cm. longas approximatis bracteis caducis subtentis; calycibus florentibus 6–7 mm. longis, in maturitate paulo auctis et labiis acuminatis hiantibus extus pilis sat crassis brevibus ut videtur purpureis unguiformis sparse conspersis, pedicellis maturis 5 mm. longis minutissime hirtellis; corollarum coccinearum tubo subsigmoideo 9 mm. longo, labia superiore vix 1 mm. longa, inferiore circiter 1.5 mm. longa ut videtur patente et emarginata; staminibus supra tubi basim 7 mm. positis et stylo glabro in tubo incluso.

ECUADOR. Loja: Near Chinche, between San Pedro and Zaruma, *Penland and Summers 1173* (type, Univ. Calif., L. A.). Taken at the same place as that of *S. curticalyx,* also described in this paper, evidently a locality not previously botanized. The occurrence of this species in Ecuador is remarkable inasmuch as it clearly establishes this section, which is chiefly Brazilian, in the northern Andes. The present species closely

resembles *S. secunda*, the type species, not only in habit but in flower structure. As nearly as one may judge from the dried corollas, the other species have a lower corolla lip which is cupped rather than deflexed. From the few flowers available it would appear that in this species the lower lip is deflexed. In the general key to the sections (p. 8–9) it might therefore be sought under 68. *Silvicolae*. The key at this point (p. 8) may therefore be modified to read as follows:

I. Stamina inter tubi medium et fauces posita saepius in tubo inclusa; corollarum labiis brevibus subaequilongis inferiore saepius incurva (*S. venosa* excepta). J. Plantae mexicanae (vide etiam *Briquetia*) 90. Curtiflorae. JJ. Plantae brasilianae vel andinae 91. *Secundae*. II. Stamina ad fauces posita; labia deflexa, etc. etc.

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The Structure of the Chloroplast and the Location of the Chlorophyll

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(WITH 11 FIGURES)

The photomicrographs[1] presented in this paper show some of the results of a series of investigations that have been made over a period of ten years on the structure of the chloroplast and the location of the chlorophyll.

The early investigations were made upon young sporophytes and young gametophytes of some twenty-five species of native ferns. Some of these are shown in figures 1, 2, 4–6. Later investigations were made upon representatives of the Thallophyta, Bryophyta, and Spermatophyta (figures 3, 7–11×). The chloroplasts of all the plants investigated were found to be made up of units (figures 2a, 9a, 10a), for which the term *plastidule* is suggested. The chloroplasts can be separated into the plastidule units (figure 2b). These plastidules are composed of globular bodies, here called *plastid granules* (figures 2c, 10c). It is possible to separate the plastidules into their respective plastid granules. The chlorophyll occurs in the colloidal substance of which each plastid granule is composed. The greenness of each chloroplast represents the sum of the color contributed by the chlorophyll of each plastid granule.

The number of plastidule units and the number of plastid granules in each plastidule vary within limits in the chloroplasts of any one plant, while the number of plastidules and their component granules in the different plant groups varies even more. For instance, the number of plastidules in the chloroplasts of *Spirogyra* sp. (figure 7c) is often three, with three or four plastid granules in each plastidule, while in *Elodea canadensis* (figure 10a) the number is above three, with forty or more plastid granules in each plastidule.

This type of chloroplast structure has been found both among plants with starch-forming chloroplasts and among plants with non-starch-forming chloroplasts. *Gladiolus* sp. and *Dahlia variabilis* exemplify plants with non-starch-forming chloroplasts, in which the chloroplast has been found to be similar to that of plants with starch-forming chloroplasts. Gladioli have five or more plastidules in each chloroplast, and five or more plastid granules in each plastidule. There are seven or more plastidules in the

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[1] The photomicrographs were taken by Mr. Louis Paul Flory, Director of the Illustration Division of the Boyce Thompson Institute of Plant Research, Inc., through the courtesy of Dr. William Crocker, Director of the Institute.

chloroplasts of the dahlia, with five or more plastid granules in each plastidule.

In those chloroplasts in which starch is made, the starch in the inmost plastid granule has been found to be the last to disappear when starch is

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Explanation of Figures 1-11

(*Fig. 1, p. 537; figs. 2–5, p. 538; figs. 6–8, p. 539; figs. 9–11, p. 540*)

Fig. 1. *Aspidium spinulosum* (O. F. Muller) Sw. Water mount of portion of frond of young sporophyte. ×1515. *a.* Chloroplast in which seven plastidules may be seen. *b.* Chloroplast dividing; in the left portion three plastidules may be seen and two in the right. *c.* Chloroplast nearer complete division; two plastidules may be seen in the portion to the left and two to the right. *d.* Chloroplast of the guard cell showing four or more plastidules.

Fig. 2. *Aspidium spinulosum* (O. F. Muller) Sw. Chloroplast and plastidules obtained by pressing cover slip of water mount of frond of young sporophyte. ×1515. *a.* Chloroplast showing three plastidules. *b.* A group of plastidules. *c.* A plastidule turned in such a way that the optical section is at the surface on the left side, while on the right it is nearer the center and shows the plastid granules of which the plastidule is composed.

Fig. 3. *Lycopersicum esculentum* Mill. Chloroplasts removed from leaf. ×1515. *a.* Chloroplast showing portions of seven plastidules. *b.* Chloroplast which shows the plastidule units. (The plastidule units of this plant are lightly held together in each chloroplast and the slightest pressure on the cover slip will resolve most of them into the plastid granule units.)

Fig. 4. *Aspidium spinulosum* (O. F. Muller) Sw. Portion of the frond of a young sporophyte. ×1515. *a.* Surface view of a chloroplast showing distinctly four plastidules. The dark areas are made by the colloidal matrix at the junction between the plastidules. *b.* Chloroplast with focus such that the plastid granules, of the four outer plastidules are shown. The focus is just below the upper plastidules of which the chloroplast is composed, and on the surface of the plastidules in the lower half of the chloroplast.

Fig. 5. *Aspidium spinulosum* (O. F. Muller) Sw. An optical focus just above that of identical area in figure 4*a*. The same chloroplast as in figure 4*a* with different focus. *b.* Chloroplasts in figure 4*b*, but now seen faintly through cell wall. *c.* A comparison of any of the identical chloroplasts as seen in the area around *c*, in figure 4 and figure 5, shows the varied appearance of a chloroplast, depending on whether the focus is at the surface, showing the plastidule units, or within the plastidule, showing the plastid granules.

Fig. 6. *Aspidium spinulosum* (O. F. Muller) Sw. Water mount of portion of young gametophyte. *a.* Chloroplast in which two plastidules are shown. *b.* Chloroplast with five plastidules.

Fig. 7. *Spirogyra* sp. The "chloroplast" is shown to consist of many chloroplasts. *a.* Chloroplast located on the edge of the band. *b.* Chloroplasts around and on the pyrenoid. *c.* Chloroplast in which two plastidule units are shown.

Fig. 8. *Polytrichum commune* Hedw. A portion of a protonema. *a.* Chloroplasts showing six and eight plastidules.

Fig. 9. *Impatiens Sultani* Hook. Portion of the epidermis showing stoma. *a.* Chloroplasts in guard cell, showing four plastidules.

Fig. 10. *Elodea canadensis* Michx. Portion of a leaf. *a.* Chloroplast showing three plastidules. *b.* A chloroplast so oriented that one plastidule lies directly on top and one on either side. The dark bands are due to light refraction from the crevice between the plastidules. *c.* Chloroplast showing, just above *c*, the boundary between two plastidules. *d.* Chloroplast showing the same as *c*.

Fig. 11. *Elodea canadensis* Michx. Portion of a leaf after treatment with iodine solution. *a.* Chloroplast showing portions of five plastidule units.

8
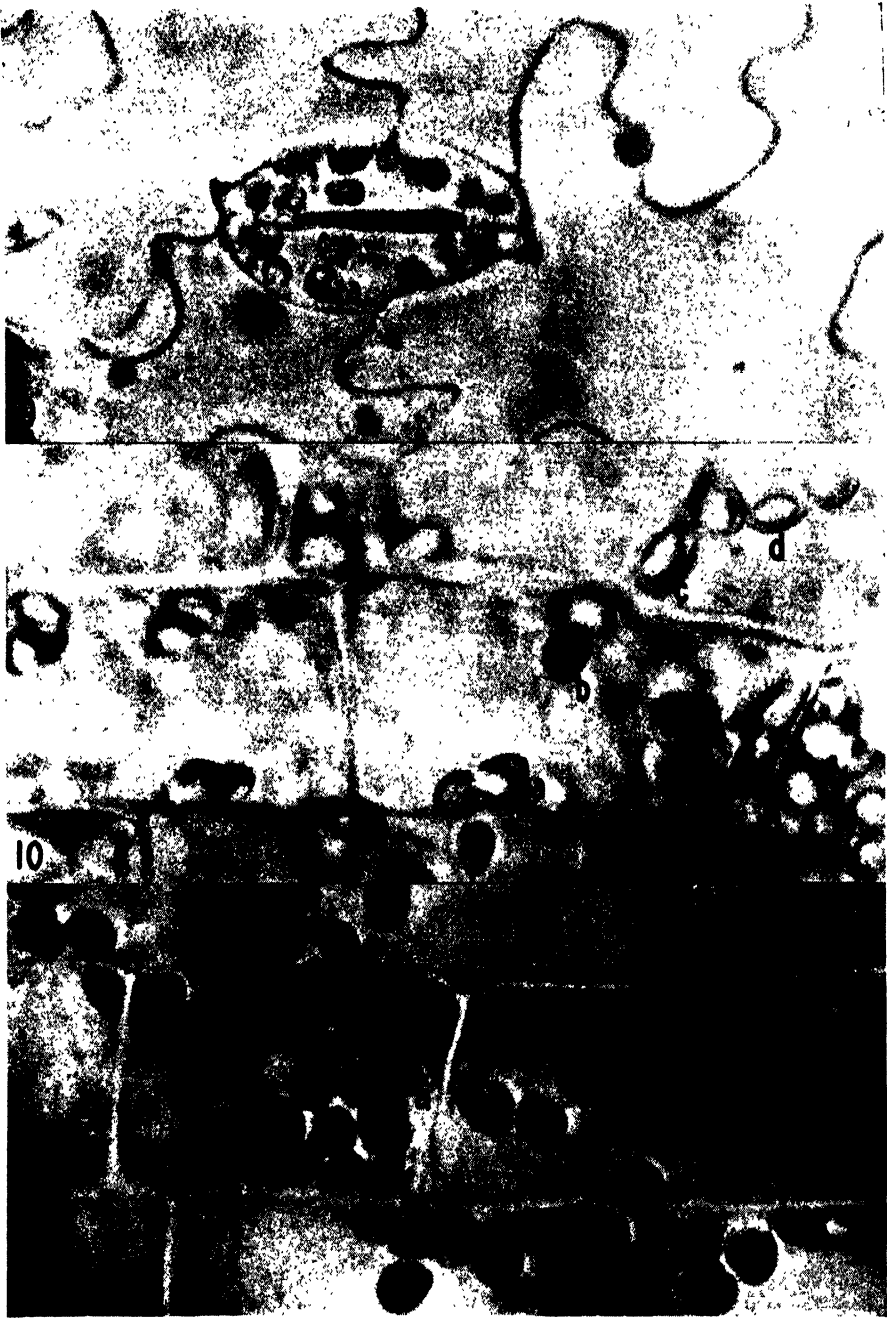
removed from the plants by storage in darkness. It is in the inmost plastid granule, also, that starch is found to be first formed when the plant is placed in light. The starch appears in the center of the plastid granules of each succeeding layer of granules, from the inner to the outer, until each of the entire series of plastid granules has within it a starch unit (figure 11*a*).

The colloidal substance of the matrix of the plastid granules remains light green after treatment with dilute iodine solution. In the photomicrographs the entire center of the plastidule (figure 11*a*) is darkened by the mass of colored starch centers in the granules, but the matrix of the outer layer of plastid granules appears as a light area at the edge of the plastidule.

A more complete report of the investigations will be published at a later date, but the many requests for the illustrations as presented at an exhibit at the meetings of the American Association for the Advancement of Science, at Columbus, Ohio, December 1939, have made it seem advisable to present them at this time.

Note:—The term "plastidule" has been used in a different sense by Ernst Haeckel and Louis Elsberg. Ernst Haeckel, however, used the term "plastid" to apply to a different portion of the cell from that now designated as a plastid, and his plastidule was a portion of what he termed a plastid; just as the term plastidule is used here to apply to a portion of what is generally termed a plastid today.

DEPARTMENT OF BOTANY
    VASSAR COLLEGE
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INDEX TO AMERICAN BOTANICAL LITERATURE

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GROWTH SUBSTANCES IN A HYBRID CORN AND ITS PARENTS

WILLIAM J. ROBBINS

(WITH FOUR FIGURES)

The inability of certain .fungi to synthesize adequate quantities of all the growth substances necessary for their complete development has suggested their growth as a means of approximating specific vitamins or vitamin-like growth substances.

Phycomyces Blakesleeanus requires for growth an external supply of thiamin or its two intermediates. Its development in a particular medium indicates the presence of thiamin or its two intermediates and the amount of growth under suitable conditions is proportional to the quantity present (6). *Ashbya Gossypii* requires an external supply of biotin (1) and the amount of its growth under proper conditions is proportional to the quantity of biotin present (5). In a medium containing an excess of thiamin the early growth of *Phycomyces* is increased by unidentified growth substances present in many materials of natural origin (2, 3, 4) and the growth of *Phycomyces* under given conditions may be used to estimate these unidentified substances.

Considerable further research is necessary before the determination of growth substances by fungi can be considered in many instances more than a crude estimate of the quantity present. Nevertheless, in the absence of other methods it has seemed desirable to determine the effect of extracts of grains at various stages of germination of a hybrid corn and its two inbred parents upon *Phycomyces* in the absence of thiamin, upon *Phycomyces* in the presence of thiamin, and upon *Ashbya Gossypii* in the absence of biotin. By these means information on differences in the quantity of various growth substances in the grains could be secured which may or may not bear on the problem of heterosis.

METHODS AND MATERIALS

The corn grains used were kindly supplied by Dr. Frederick D. Richey. *W F 9* and *38–11* are inbreds developed at the Indiana Agricultural Experi-

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ment Station and are among the better lines in the corn belt. Both are vigorous for inbreds; *W F 9* is earlier and makes a stockier growth, whereas *38–11* is later, taller and has a very spindling growth particularly for the first 30 days. Both have unusually good root systems for inbreds and are used extensively in hybrids. The combination *W F 9 × 38–11* is used as the seed parent of *U. S. hybrid 13* and of a number of other less well known hybrids. All seed was of the 1938 crop.

The procedure was as follows: A definite number of grains (about 20) was placed with 5 ml. of distilled water in Petri dishes at 25° C. After 24, 48 or 72 hours the grains were separated into embryo and endosperm, ground in a mortar and extracted with 50 ml. of 5 per cent pyridine for 24 hours at room temperature. The supernatant fluid was decanted, evaporated by boiling on a hot plate to small volume, centrifuged and the supernatant liquid made up to volume with distilled water so that 1 ml. represented the extract from 1 embryo or 1 endosperm.

For estimating thiamin and its intermediates *Phycomyces* was grown 8 days at from 23° to 25° C. in 25 ml. quantities of solution I,[1] to which various quantities of the corn extracts were added.

For estimating the unidentified growth substances *Phycomyces* was grown about 70 hours at from 23° to 25° C. in 25 ml. quantities of the above solutions plus 0.5 mg. thiamin per liter and various quantities of the corn extracts.

For biotin *Ashbya Gossypii* was grown 9 days at from 23° to 25° C. in 25 ml. quantities of solution I plus 0.2 g. M-inositol and 0.5 mg. thiamin per liter.

EXPERIMENTAL RESULTS

Experiment 1. Twenty-two grains of each parent and the hybrid were germinated for 24 hours and extracted as described above. *Phycomyces* was grown 75 hours in solution I plus 0.5 mg. thiamin per liter. The extract of 0.025 or 0.25 of an embryo or endosperm was added per flask. The experiment was run in duplicate. The dry weights of the mycelium for a pair of flasks are given in table 1.

The growth in the solutions containing extracts of embryos of the hybrid was greater than that in the solutions containing extracts of the inbred parents. The same was true for extracts of the endosperm. The growth in the solutions with extracts of embryos of *W F 9* was greater than in solutions containing extracts of embryos of *38–11;* while this order for the parents was reversed for extracts from the endosperm.

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[1] Solution I contained per liter 50 g. dextrose, 2.0 g. asparagine, 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7 H_2O$, 0.5 mg. thiamin, and the following trace elements: 0.005 p.p.m. B, 0.02 p.p.m. Cu, 0.1 p.p.m. Fe, 0.01 p.p.m. Ga, 0.01 p.p.m. Mn, 0.01 p.p.m. Mo, and 0.09 p.p.m. Zn.

TABLE 1

Dry weight of mycelium of Phycomyces in a pair of flasks, grown 75 hours in a solution of mineral salts, sugar, asparagine and thiamin plus the extract of embryo or endosperm of corn grain of the inbred parents and hybrid.

Extract added per flask	Dry wt. of mycelium, mg.		
	38–11	*W F 9*	*W F 9 × 38–11*
0.025 embryo	5.5	8.5	14.0
0.25 embryo	14.0	15.0	16.2
Total	19.5	23.5	30.2
0.025 endosperm	7.4	5.7	9.8
0.25 endosperm	13.9	13.2	16.4
Total	21.3	18.9	26.2
Control	11.5	11.5	11.5

Experiment 2. Experiment 1 was repeated with the extract of 0.25, 0.5 and 1.0 embryo or endosperm per flask and a growth period of 67 hours. The results were similar to those found with the smaller quantities of extracts and somewhat shorter growth period.

Experiment 3. Twenty grains of each parent and the hybrid were germinated for 48 hours. *Phycomyces* was grown 67 hours in solution I plus 0.5 mg. thiamin per liter. The extract of 0.25, 0.5 or 1.0 embryo or endosperm was added per flask and the experiment was run in duplicate. Again the growth of *Phycomyces* in solutions containing extracts of the embryo and of the endosperm of the hybrid was greater than in those containing extracts from either parent (figs. 1 and 2). Again the extract from the embryo of *W F 9* was more effective than that from *38–11* while the order for the parents was reversed for the endosperm extracts. The endosperm extracts .were more effective than those from the embryos. The growth in the solutions containing extracts was in every instance greater than that in the check solution (8.5 mg.).

Experiment 4. Three lots of 20 grains of each parent and the hybrid were placed under conditions for germination. Extractions were made at the end of 24, 48, and 72 hours.

The air-dry weights of the various lots of corn grains were as follows. For those germinated 24 hours: *38–11*, 5.150 g.; *W F 9*, 5.150 g.; *W F 9 × 38–11*, 4.750 g. For those germinated 48 hours: *38–11*, 5.275 g.; *W F 9*, 5.000 g.; *W F 9 × 38–11*, 4.975 g. For those germinated 72 hours: *38–11*, 5.125 g.; *W F 9*, 5.150 g.; *W F 9 × 38–11*, 5.050 g. The hybrid corn was more vigorous in its germination than either parent. At the end of 24 hours all grains were swollen but no roots or shoots had appeared. At the end of 48 hours, *38–11* had 12 grains with roots 1 cm. long and 8 with roots just break-
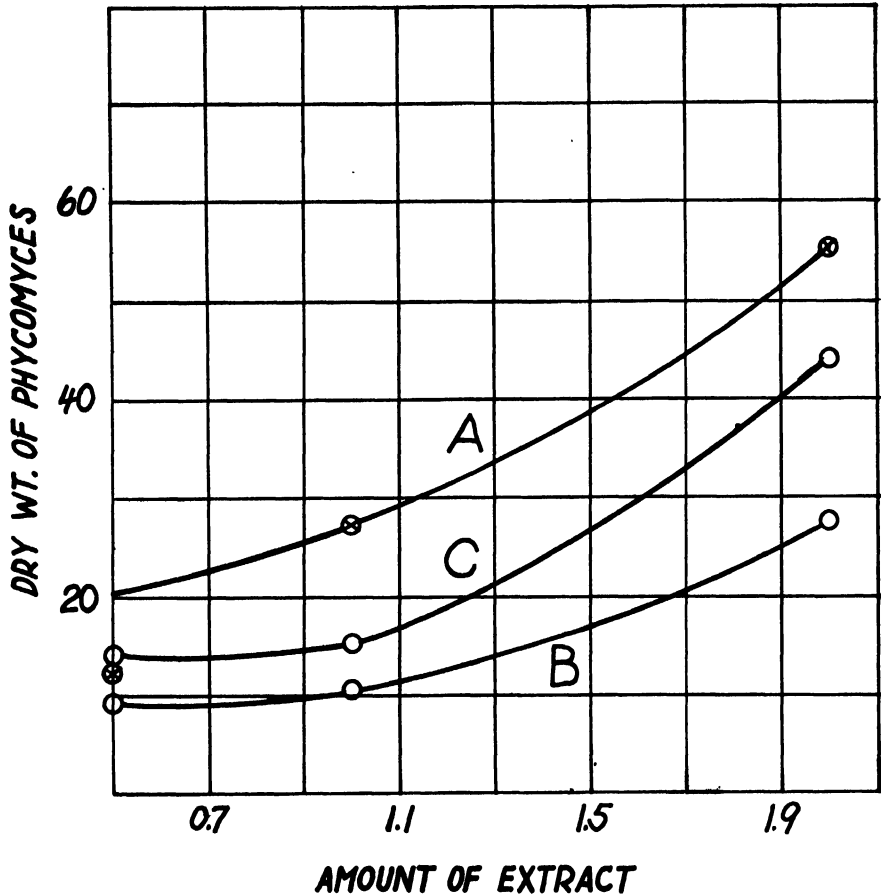
FIG. 1. Dry weight of *Phycomyces* grown in solution of sugar, asparagine, mineral salts and thiamin plus extract of 0.25, 0.5, or 1.0 embryos of a hybrid corn (A) and its inbred parents (B = *38–11*, C = *W F 9*). Corn germinated 48 hrs. Weight of mycelium grown without extract, 8.5 mg.

ing out; *W F 9*, 10 grains with roots 1 cm. long, 7 with roots 0.5 cm. long and 3 just breaking out; *W F 9 × 38–11*, 16 grains with roots 1–2 cm. long and 4 with roots 0.5 cm. long. At the end of 72 hours *38–11* had roots 1–2 cm. long and faintly green shoots about 0.5 cm. long; *W F 9*, 14 with roots 1–1.5 cm. long, shoots 0.2–1.0 cm. and 6 with short roots but no shoots; *W F 9 × 38–11*, all grains germinated with roots 2–4 cm. long and green shoots 1–2 cm. long.

The extract of 0.5 embryo or endosperm was added to 25 ml. of solution I containing 0.5 mg. thiamin per liter and *Phycomyces* was grown for 72 hours.
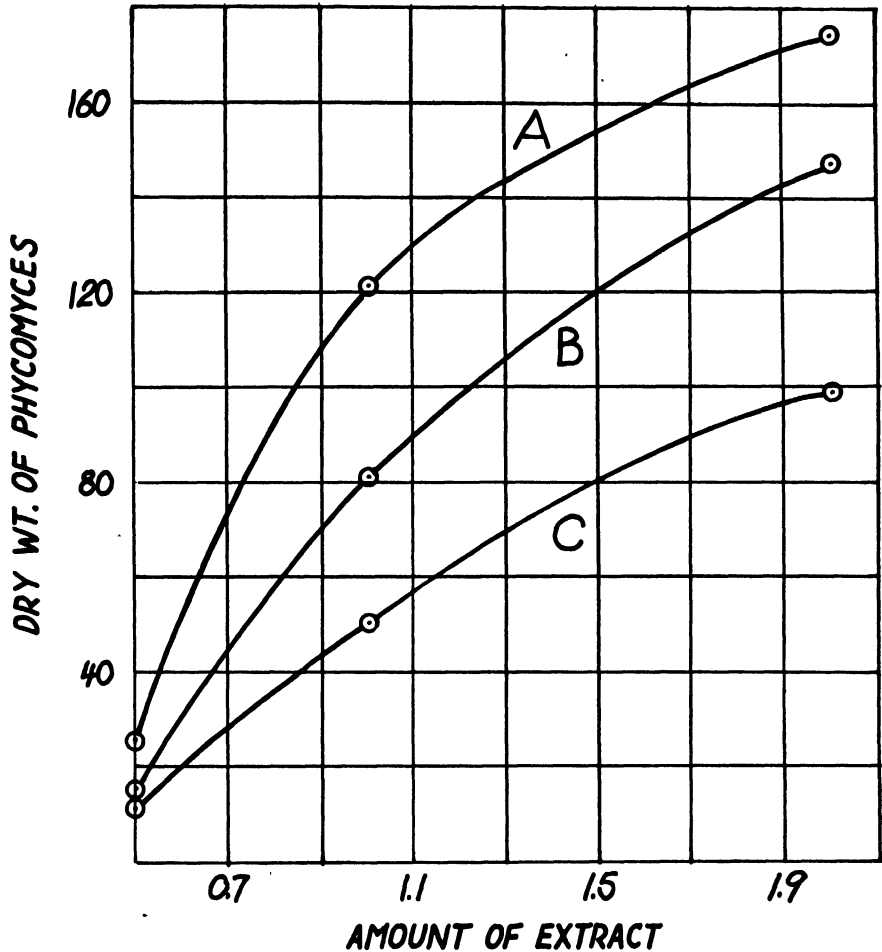
Fig. 2. Dry weight of *Phycomyces* grown in solution of sugar, asparagine, mineral salts and thiamin plus extract of 0.25, 0.5, or 1.0 endosperms of a hybrid corn (A) and its inbred parents (B = *38–11*, C = *W F 9*). Corn germinated 48 hrs. Weight of mycelium grown without extract, 8.5 mg.

The results in this experiment (figs. 3 and 4) were more irregular than in experiments 1, 2, and 3. For example the determination for the extract of the endosperms for *W F 9* after 48 hours and of *38–11* after 72 hours germination do not fall on the curves (fig. 4). Nevertheless, it appears that the extracts of the hybrid embryos and endosperm were more effective than those of the inbred parents for all three periods of germination. Again the extracts of the embryos of *W F 9* were more effective than those of *38–11* and the order was reversed for the endosperm extracts. The extracts from the endosperm were more effective than those from the embryos. The effec-
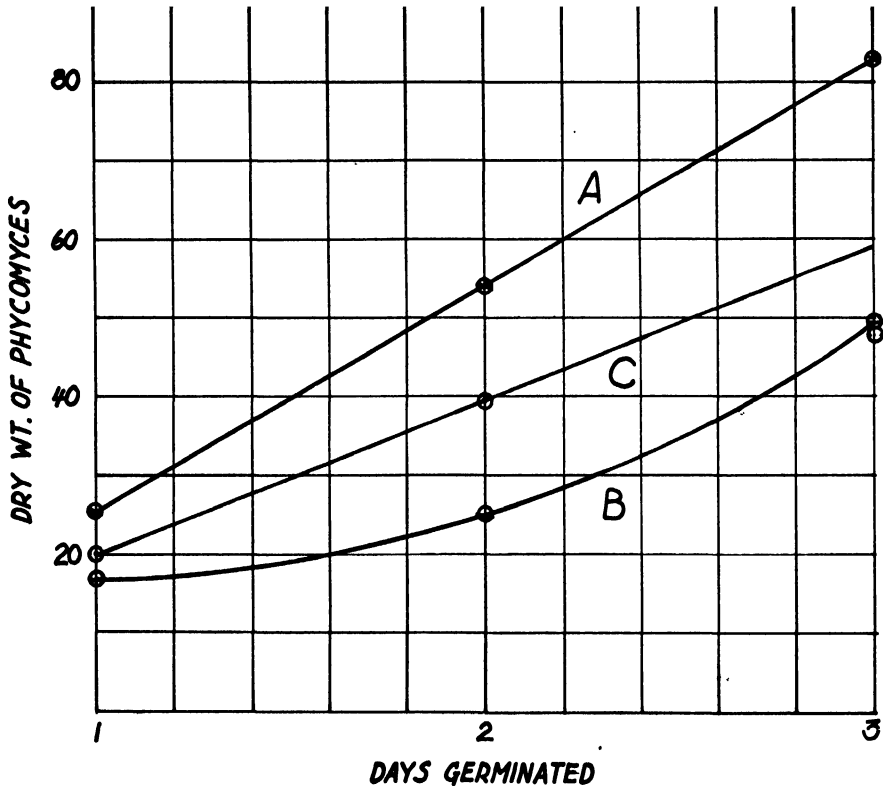
FIG. 3. Dry weight of *Phycomyces* grown in solution of sugar, asparagine, mineral salts and thiamin plus extract of 1 embryo of a hybrid corn (A) and its inbred parents (B = *38–11*, C = *W F 9*). Grains germinated 1, 2 and 3 days. Weight of mycelium grown without extract, 9.1 mg.

tiveness of the extracts of both embryos and endosperm increased with length of time of germination. The growth in the solutions containing the extracts was in every instance greater than that in the check solutions (9.1 mg.).

Experiment 5. The extracts prepared in experiment 3 were used in this experiment. *Phycomyces* was grown 8 days in solution I supplemented with the extract of 0.5 or of 1 embryo or endosperm per flask. To some flasks of each extract 10×10^{-9} gram-mole of thiamin pyrimidine was added, to others 10×10^{-9} gram-mole of thiamin thiazole. All solutions were in duplicate. Since the basic solution in this instance contained no thiamin the growth of *Phycomyces* depended upon the thiamin or its intermediates present in the extracts. The growth of *Phycomyces* in these solutions (table 2) shows that the extracts from the embryo contained much more thiamin than those from the endosperm. The *38–11* embryos contained more than *W F 9* embryos and the hybrid embryos least. All the embryos contained an excess of pyrimidine,
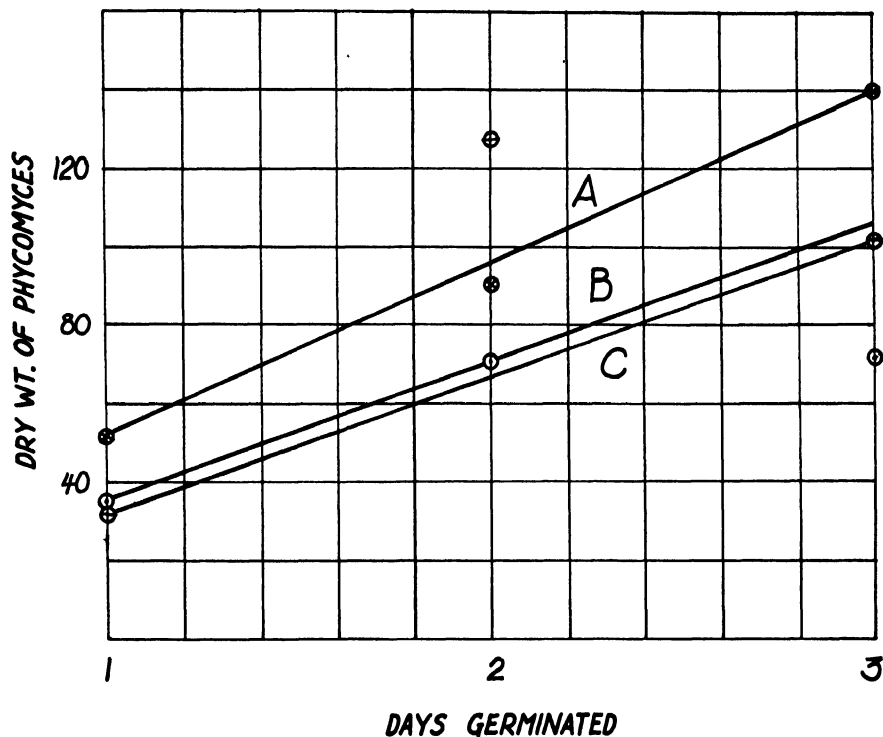
FIG. 4. Dry weight of *Phycomyces* grown in solution of sugar, asparagine, mineral salts and thiamin plus extract of 1 endosperm of a hybrid corn (A) and its inbred parents (B = *38–11*, C = *W F 9*). Grains germinated 1, 2 and 3 days. Weight of mycelium grown without extract, 9.1 mg.

as is shown by the greater growth in those solutions to which thiazole was added.

The extracts of the endosperm of *38–11* contained the least thiamin and those of *W F 9* and the hybrid about the same. There seemed to be little or no accumulation of pyrimidine in the endosperm.

Experiment 6. The extracts from experiment 2 were used in this experiment. *Ashbya Gossypii* was grown for 9 days. The experiment was performed in duplicate and the dry weights in table 3 are the average of two cultures. It appears that there was somewhat more biotin in the embryos than in the endosperm, though except for *W F 9* the difference was not great. The embryo extracts of *W F 9* were most effective and those of *38–11* least. For the endosperm extracts those of the hybrid were most effective and those of *38–11* least. The quantity of biotin present in the extracts was estimated from the curve given by Robbins and Schmidt (5) which was based on data from Kögl and Fries (1).

TABLE 2

Growth of Phycomyces per flask in a solution of mineral salts, sugar and asparagine supplemented with extracts of embryo or endosperm of corn grains germinated 48 hours. Some solutions contained in addition 10 × 10⁻⁹ gram-mole of vitamin pyrimidine and some 10 × 10⁻⁹ gram-mole of vitamin thiazole.

Extract added	Dry wt. mycelium, mg.		
	Basic solution	Basic solution plus pyrimidine	Basic solution plus thiazole
0.5 embryo			
38–11	134.7	142.5	204.7
W F 9	115.9	121.0	166.1
W F 9 × 38–11	91.9	107.9	149.1
1.0 embryo			
38–11	239.7	256.4	304.6
W F 9	197.1	206.3	252.0
W F 9 × 38–11	153.7	175.7	240.6
0.5 endosperm			
38–11	12.5	14.7	22.1
W F 9	23.1	35.5	30.2
W F 9 × 38–11	22.7	28.9	32.3
1.0 endosperm			
38–11	22.2	21.0	30.9
W F 9	33.9	61.0	49.5
W F 9 × 38–11	33.7	55.1	47.6
Control	3.3	3.3	3.3

TABLE 3

Growth of Ashbya Gossypii per flask in solutions supplemented with extracts of a hybrid corn and its inbred parents. Biotin calculated from growth of Ashbya is also given.

Extract supplement	Dry wt. of *Ashbya*, mg.			Biotin in extract in 10⁻⁹ gram-mole		
	38–11	*W F 9*	*W F 9 × 38–11*	*38–11*	*W F 9*	*W F 9 × 38–11*
0.5 embryo	4.6	10.7	9.9	2.05	8.2	6.6
1.0 embryo	11.5	18.0	14.9	9.0	19.0	13.5
0.5 endosperm	4.5	5.8	8.5	2.0	3.0	5.7
1.0 endosperm	....	8.6	14.1	....	5.7	12.5
Control	0.1	0.1	0.1	none	none	none

DISCUSSION

From the determinations described in the preceding pages it appears that extracts of the partially germinated grains of a hybrid corn (*W F 9 × 38–11*) had per grain a greater beneficial effect upon the early growth of *Phycomyces* in the presence of thiamin than those of either of its inbred parents (*W F 9*

and *38–11*). Since the solution in which the beneficial effect of the extracts was found contained sugar, asparagine, mineral salts and thiamin it seems probable that their beneficial effect was produced by unidentified growth substances which have been discussed elsewhere as factor Z (4). Inhibitory substances also were probably present in the extracts since a smaller dry weight was produced in some instances in the presence of the extract than in its absence (table 1). However, with the larger amounts of the extract growth was materially greater than in the check solutions, demonstrating the presence of beneficial materials.

If the amount of factor Z can be estimated from the effect of the extracts on the early growth of *Phycomyces* in the presence of thiamin then the following generalities seem permissible. The amount of factor Z increased with the time of germination, at least up to 72 hours germination. The quantity was greater in the extracts from the endosperm than in those from the embryo. The quantity was greater in the extracts from the endosperm of *38–11* than from that of *W F 9* but greater in the embryo of *W F 9* than in that of *38–11*. The quantity was greater in the grains of the hybrid than in those of either parent.

The amounts of thiamin and its intermediates in embryo and endosperm of the grains of the hybrid and its parents were not correlated with the amounts of factor Z. Neither did the amount of biotin in the extracts appear to be correlated with the amount of factor Z; for example, there was more factor Z in the endosperm than in the embryo while the reverse was true for the amount of biotin.

Is factor Z of significance in relation to the problem of heterosis? A positive answer to this question would imply that the growth of both hybrid and parents is limited by the quantity of factor Z which each synthesizes, and that the hybrid synthesizes a greater amount than either of its parents. Such an assumption is not improbable; the accumulation of reserve food in green plants suggests that their growth is frequently not limited by the food available but by their ability to use it, which depends, in part, upon the supply of vitamin-like growth substances. It is obvious, however, that a conclusion so fundamental and far-reaching cannot be made upon the basis of a single hybrid and its parents. Furthermore, even if the grains of other hybrids and their parents should be found to differ as the ones do which are reported in this paper evidence is still needed to show that factor Z is not the result of the growth rather than causally associated with it as a limiting factor. Nevertheless, the results are suggestive and the possibilities deserve further exploration.

SUMMARY

The effect of extracts of partially germinated grains of a hybrid corn and its inbred parents was determined on the growth of *Phycomyces* in the

absence of thiamin and in the presence of thiamin and on the growth of *Ashbya Gossypii* in the absence of biotin. The extracts of the grains of the hybrid had a greater effect on the early growth of *Phycomyces* in the presence of thiamin than had those of either parent. The extracts of the hybrid did not have the greater effect on *Phycomyces* in the absence of thiamin nor on *Ashbya* in the absence of biotin. The possible relation of these results to the phenomenon of heterosis is briefly discussed.

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THE ECOLOGY OF RARE PLANTS

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Rare plants, though the chief interest of taxonomists, have been almost wholly ignored by ecologists. This is easy to understand. The collector journeys far to get rarities to complete his herbarium, but since they seem to cut no figure in the vegetation as a whole, they do not ordinarily enter the horizon of the ecologist at all. Yet I believe the study of rare plants can add much to our understanding of ordinary vegetation; for I have come to think that the explanation of the occurrence of rare plants, which has puzzled botanists from time immemorial, will contribute to an understanding of the vegetational history of their habitats.

Certainly rare plants in many cases are not isolated, individual phenomena, but their presence is a characteristic feature of the ecology of the areas in which they occur; for it is a curious fact that rarities grow together, certain areas being especially rich in plants not to be found elsewhere for long distances. Every working botanist will call to mind cases from his own experience. The problem of the ecologist, then, is to ascertain the reason for the congregation of rarities into special localities. In this paper there is offered for more general testing a working hypothesis for the concentration of rarities together with the data which suggested it.

DIFFERENT TYPES OF RARE PLANTS

Various types of rare plants come readily to mind. Some, like the Sequoias and Torrey pines of California, occur only in very restricted localities. Others, like the Devil Club of the Pacific northwest coast, are common enough over a wide stretch of country but have also a few small outlying stations far distant from the main body of their ranges—for the Devil Club, Isle Royale in Lake Superior.

Some of those closely restricted today, like *Sequoia*, are shown by fossils to have once covered vast areas and many others, like the Torrey pines, may safely be assumed to be the last slowly dying vestiges of races once widespread. The outliers are generally believed to be relics of ranges once continuous and this interpretation is in many cases supported by fossils (Berry 1924). Others of restricted occurrence have close relatives that are widespread in other regions, which makes it appear that the local endemic is a relic which has been modified after separation from its relatives, and many such endemics have changed so little from the original that their differences would have passed unnoticed except for their geographical isolation.

Other rare plants are mutants recently arisen in the midst of the parent species. These evidently are very young types, whereas the first mentioned are old, even though specific distinctness may have been only recently or only partly attained. In this paper, only the old types are considered.

WHAT MAKES A SPECIES RARE?

To give a specific reason in terms of the factors involved why one species is rare while a related and apparently similar one is abundant is quite beyond the present attainments of ecology. A formulation of the reason in general terms is, however, readily made, but such a statement is so clearly a recital of the obvious that it may seem useless. Yet it can lead us a good way in our quest of an understanding of rarity. The difference between a rare species and a common one lies in the fact that the one fails or almost fails to establish its progeny in the competition for its habitat where the other succeeds in so doing.

The explanation of rarity must, therefore, lie in an evaluation of the competitive competency of species.

Up to the present, ecology has been so much taken up with consideration of the physico-chemical factors of the habitat that it has given little attention to competition. Yet competition[2] is probably the most important cause of succession. This statement may be challenged when it is recalled that succession usually involves a series of habitats as well as a series of species— hydrarch from open water to rich soil, etc. This .physiographic aspect of ecology has, of course, great significance, and is likewise of importance in the ecology of rare plants. But if we allow for this, competition probably exerts a greater influence on succession than habitat.

MEANS OF EVALUATING PLANT COMPETITION

In the ordinary succession seen in nature, habitat factors and competition factors are so inextricably intertwined that neither group can be isolated for separate observation. But in the revegetation of man-made clearings, especially when they are denuded by plowing, and their return to the climax, competition may be observed alone, for in this case there is no change in the habitat.

Species which are early displaced in ˙the secondary successions of old fields are clearly of low competitive capacity as compared with members of

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[2] Even the term competition has been only loosely defined in recent ecological literature. I use it as including the whole struggle for existence so far as that is conditioned by biotic factors. Whenever two individuals come close enough together to interfere with each other's activities or development they enter into competition. Reflection will show, I believe, that any narrower conception of competition, such as the attempt to limit competition to the struggle between organisms of approximately equal competence, cannot be maintained.

the permanent vegetation. Membership in the climax that finally takes possession is determined by little else than competitive capacity—e.g., in our northern hardwood forest, by shade tolerance. If one compare the places taken by the various species in the old field succession with their places in the natural succession, he can estimate competitive conditions in natural habitats.

"HABITAT CHOICE" AS AN INDICATOR OF COMPETITION

Another indication that competitive competency rather than habitat factors controls the occurrence of rare plants is given by the perplexing inconsistency of "habitat choice" by rare plants. An aquatic such as *Cabomba* grows submerged wherever found, and we can be assured that submergence is one of the necessary requirements in its habitat. Similarly when one factor is always present in the habitat of a rare species we set it down as a requirement. But there is no regularity in the character of the places where many of the rare plants occur.

In the Bruce Peninsula of Ontario, one of the most notable conservatories of rare plants, Stebbins (1935) reports: "The contrast between boreal and southern types in the same association was made more remarkable by the presence of calciphiles and acid loving plants both equally at home. Limestone barrens covered with *Pinus banksiana* and *P. resinosa* supported *Danthonia spicata, Arctostaphylos Uva-ursi* var. *coactilis* and *Coreopsis lanceolata* along with such marked calciphiles as *Anemone multifida* var. *hudsoniana, Habenaria unalascensis, Senecio obovatus,* and *Asplenium viride.*" Just how remarkable this congregation of rarities is may be judged by one unfamiliar with the species named by looking up their ranges in the Manual. It is emphasized by the fact that Fernald (1919) once wrote a paper entitled "Lithological Factors limiting the Ranges of *Pinus Banksiana* and *Thuja occidentalis*" in which he assembled much data to show that *Pinus Banksiana* throughout its range, at its southern limits as well as in the north, consistently avoids limestone—exactly the habitat in which it occurs on the Bruce Peninsula; while *Thuja* is equally restricted to limestone. On Bruce they grow almost side by side. I may add that I have verified Stebbins' report with my own eyes. Apparent inconsistencies of this sort are characteristic rather than exceptional in the occurrence of rare plants.

CLIMATE AND COMPETITION AS FACTORS IN PLANT DISTRIBUTION

Stebbins' perplexity brings to the fore another factor in plant distribution. It is commonly believed that it is climate that fixes the limits of plant ranges. While there can be no manner of doubt but that climate sets a limit beyond which a species cannot go, many species do not go as far as climate, if competition were eliminated, would permit.

The Venus fly-trap is one of the rarest of plants, confined to a restricted area on the Carolina Coastal Plain in a "mesothermal" climate. Some years ago it was planted near Washington, D. C., somewhat more than 300 miles north of its northernmost native station in a "microthermal" climate. It persisted and did well without assistance though not in conditions ideal for it, until pulled up by over-enthusiastic botanizers. It is particularly noteworthy that it survived without injury the winter of 1933–34 which broke all recent records for severity and duration. The same species planted in a sand-gravel bog in Westmoreland County, Virginia, 250 miles beyond its natural range, is likewise doing well.

TREES PLANTED BEYOND THEIR NATURAL LIMITS

But it is not necessary to have recourse to experiments with rare plants to demonstrate that species frequently have not attained in nature the dispersal permitted by climate. Wide and varied experience in planting trees beyond their natural limits brings abundant testimony to the fact. Robert Bell (1897) reports that the black walnut, which is native to Canada only along the north shore of Lake Erie, grows well and forms wood rapidly near the city of Quebec, 500 miles northeast of its nearest native stations, while at Carlton Place, 200 miles from native trees, it ripens its nuts. The honey locust and Kentucky coffee tree are native no further north than Pelee Island in Lake Erie, but the former flourishes well throughout the peninsula of Ontario and down the St. Lawrence nearly to Montreal, while the latter grows to maturity at Ottawa. These places are five hundred and twenty-five and four hundred and twenty-five miles respectively from Pelee Island. "The black ash proves quite hardy at Moose Factory on James Bay more than 100 miles north of its present range and where it is exposed to the chilling influence of sea air."

The common experience is, of course, that such trees require nursery culture, i.e., protection from competition during their early stages, and thus makes it clear that it is competition rather than climate which prevents their unassisted spread in nature.

It is pertinent to point out in this connection that crop plants find both habitat and climate entirely congenial as long as weeds are kept away but most of them are utterly unable to spread spontaneously against the competition of wild species.

RARITIES OF OCEANIC ISLANDS

We may recall that the most notable of rare species, both plant and animal, are to be found on remote islands in the ocean. These are refugees to which the competition of the continents does not reach. Among animals, whose competitive relations are easier to observe than those of plants, it

can sometimes be demonstrated that their preservation is in fact due to the absence of enemies. The remarkable giant tortoises from which the Galapagos Islands take their name, for example, would stand in imminent danger of extinction from dogs run wild on the islands even if human slaughter were stopped. It is significant (1) that similar tortoises occur elsewhere only on certain islands of the Indian ocean, e.g., Mauritius, and (2) that closely related forms once existed on the continents, as is shown by fossils. Their preservation on islands is clearly due to the absence of predacious animals.

ALPINE RARE PLANTS

Next to insular types, the alpines constitute probably the most numerous class of rare plants. In these also there are indications that it is competition that is the crucial factor in their occurrence.

Most of the alpine species are also arctic; the predominant characteristic of arctic, especially of high arctic vegetation is the absence of the closed associations produced by competition that are found in the vegetation of temperate latitudes. Evidence that there is little competition among alpine plants comes from two directions (Griggs 1934a) :

First, arctic-alpine plants have no specific structural adaptations for their habitats, such, for example, as the well-known morphological peculiarities of water plants. If, for example, one were given fragments of a water-lily leaf with its conspicuous air passages and stomata on the upper surface or a submerged leaf of *Vallisneria* with large air spaces and no stomata, he would have no difficulty in assigning the material to an aquatic habitat. But if he were given fragments of *Alnus crispa, Oxyria digyna, Geum Peckii, Viola palustris, Arctostaphylos alpina,* or *Pinguicula vulgaris,* he could never guess that in their southern stations all are confined to the immediate vicinity of our highest mountains. It might be objected that these species, though geographically limited in our eastern states to mountains, frequent habitats which occur in the lowlands as well. Why then should they be confined to the mountains?

Empetrum and *Ledum,* whose habitats are more characteristic of the alpine zone, have highly specialized leaves, but both occur in lowland as well as upland. Nor do the species which colonize the bleakest and most exposed summits make a much better showing. *Arenaria groenlandica, Carex concolor,* and *Juncus trifidus* grow in extreme habitats, but there is nothing in their histology not duplicated in their lowland relatives.

This situation is well known and has been specifically elaborated for arctic plants by Holm (1922). But the meaning of it has not been sufficiently emphasized. While it is perfectly true that the low herbs and prostrate shrubs characteristic of arctic and alpine habitats are suited to the wind-swept situations where they grow and so have attained a sort of climatic

adjustment, that is only the negative side of their ecology. There is no indication that they prefer severe climates. Everything we know indicates merely that they can *tolerate* conditions too adverse for other plants.

ALPINE PLANTS IN RIVER GRAVELS

Second, characteristic alpine plants are not confined to high altitudes but often occur in the lowlands as well. And when they occur in the valleys they are often more thrifty than on the summits, thereby strengthening the belief that they do not prefer alpine conditions but are forced into them by competition. I will give only three illustrations.

In Glacier National Park Standley (1921) reports: "*Epilobium latifolium* is certainly a typical plant of alpine meadows and rock slides, but it is found at many places along streams at low altitudes, often in considerable abundance and in greater luxuriance than at high altitudes. Along the creek at St. Mary, *Dryas Drummondii* is more abundant and more vigorous than above timberline, yet it is evident to any botanist that the plant is there only by accident. Along the creek at the east entrance many stray plants of alpine species may be found." While mentioning the species it should be pointed out that *Dryas Drummondii* is one of the rarest of plants in eastern America, being known only from the Mingan Islands, the Gaspé Peninsula, and the Slate Islands of Lake Superior (Fernald 1925, 1935; Marie-Victorin 1932). I may add that I have personally observed that the situation reported by Standley obtains as far north as Jasper. In Gaspé, *Dryas Drummondii* is shown by Marie-Victorin (1938, p. 541) "pioneering on the calcareous gravels of the Petite Cascapedia River" in company with balsam poplar.

Raup reports (1934) that in the Peace River region no less than 40 species from above timberline reappear at low elevations. "Most of these inhabit damp sandy or muddy banks very close to the water's edge where they are inundated in flood times; making their habitat exceedingly unstable and the existence of any plants at all quite hazardous." Clearly their two habitats have little resemblance in climate or physical characteristics. Two factors, however, they do possess in common: (1) "Life for any plants at all is quite hazardous," and (2) "The forest is unable to invade them"; in the one case "on account of flooding and the general instability of the soil," in the other on account of the severity of climate. Both are free from the competition of trees, and this I take to be the determining factor.

Like the new stream banks, the alpine habitats stand near the pioneer stage of the ecological succession. A survey of non-alpine rare plants shows that a majority of those in our territory occur in habitats low in the succession. It is really surprising how frequently one finds rare plants growing in rocky places, cliffs or their talus, on shores, in bogs or in sand barrens.

THE CURIOUS "PREFERENCE" OF RARE PLANTS
FOR SHORE HABITATS ·

Empetrum nigrum on Mt. Desert Island occurs in two places: the mountain summits and the sea shore (Moore and Taylor 1927). On the sea cliffs it actually competes with the halophytes especially adapted to endure salt spray. I found it there growing in the same little pocket of soil with the seaside plantain, *Plantago decipiens,* their roots intertwined. It cannot compete with other species in habitats where trees can grow and so is crowded to the edges of the forest both above and below the woods.

Cypripedium passerinum, one of the rarest of species in eastern America, was found by Marie-Victorin in the Mingan Islands "on the gravel spit by the seashore within reach of the tide" (Marie-Victorin 1928, and 1938, p. 537). His photograph shows a typical beach, a place where one would expect *Arenaria peploides, Mertensia maritima, Lathyrus maritimus, Elymus arenarius,* and *Senecio Pseudo-Arnica.* Only part of the ground is occupied by vegetation of any sort. In the Rocky Mountain region, where this species is widely distributed, it grows in rich spruce woods (Jennings 1919). Naturally Marie-Victorin was very much perplexed at its occurrence on the beach. It is difficult to imagine any physico-chemical feature of the Mingan beach that specially fits it for *Cypripedium passerinum.* Marie-Victorin has recourse, but without much conviction, as he later states, to an idea that the presence of sodium chloride in the soil may in some way favor transpiration. But the one obvious advantage which the beach offers is the same freedom from competition that is enjoyed by plants in a garden. Is it not altogether probable that the cause of their presence lies just here?

A surprising number of the rare plants of the St. Lawrence Basin are confined to the unstable ground along rivers or tidal marshes. I will cite five more examples:

(1) *Aster gaspensis,* the sole eastern representative of a widespread group of western species, known only from the bare gravels of a steep river bank where again the existence of any plant is rendered precarious from alternate inundation and ice action (Marie-Victorin 1932).

(2) *Lathyrus nevadensis* is known in the east only from a somewhat similar situation where it grew with *Dryas Drummondii* (Marie-Victorin 1932).

(3) *Cirsium minganense* almost parallels *Cypripedium passerinum* except that it is judged to be specifically rather than varietally different from the widespread *C. foliosum,* a mesophyte inhabiting the humid valleys of the Rocky Mountains. It also grows with *Lathyrus maritimus* and *Elymus arenarius* on the beaches (Marie-Victorin 1925).

(4) *Gentiana victorini* (Marie-Victorin 1925), and (5) *G. gaspensis* (Marie-Victorin 1932), are confined to tide-lands in Quebec, again unstable

habitats where vegetation is kept close to the pioneer stage by occasional inundations from storms, by surf, or by ice shove in winter.

RARE PLANTS OF BRITAIN LARGELY COASTAL

"It is noticeable that a great part of the rare British plants occur close to the coast . . . though they are not maritime species," says C. Reid as quoted by Marie-Victorin (1928). He offers two explanations:

First, that they have only recently arrived from the continent and naturally landed near the coast. To this, Marie-Victorin very properly points out (a) that no such explanation would hold for the American plants cited and (b) that the rare plants occur on both coasts of Britain, the most distant as well as that nearest to the continent.

Reid's second explanation seems to me the correct one—namely, "on the coast alone do we find any considerable extent of bare land—practically garden land—which does not at the same time consist of poor soil. The tumbled under-cliffs of our coast are just the place to give a foreign invader a chance."

HABITATS OF RARE PLANTS USUALLY LOW IN THE ECOLOGICAL SUCCESSION

Only a few of the rare plants of Gaspé which occur on river banks or tide flats where vegetation is held close to the pioneer stage by the frequent destruction of its members, have been mentioned. It is surprising to observe that of the remainder comparatively few grow on the high mountain plateaus which, because they show no evidence of ice action, have been supposed to have remained bare not only of ice but also of snow during the Wisconsin glaciation, and thus as nunataks to have furnished a refuge for all these rare species (Fernald 1925; see also Wynne-Edwards 1939). On the contrary most of the rarities are confined either to the sea cliffs, to the crests of the roughest hills, or to deep ravines (like the Devil's Gulch on Mount Albert). Rousseau (1933) trenchantly inquires why, if these plants survived the Wisconsin climate on the summits, they should have abandoned these habitats for the lowland on the return of more genial conditions. West Bluff, the most famous station for rare plants on the Keweenaw Peninsula, is formed by a rotten, rapidly crumbling conglomerate. These are all places which are eroding too rapidly to permit the formation of soil and so, like the beaches, are held in the pioneer stage of succession. Where the surface is sufficiently stabilized for soil formation, the forest enters and any rare species present is driven out through inability to compete.

In all of these habitats—whether river gravels, sea beaches, tide flats, or cliffs—life for the individual plant is precarious, as I have determined over and over again by carrying on, year after year, observations on marked

quadrats in the study of the revegetation of areas covered by the ash of Katmai.

ECOLOGY OF ASSOCIATES OF RARE SPECIES

Clues to the ecological status of rare species may often be obtained from examination of the species associated with them in the same habitat.

On Bruce Peninsula *Polystichum lonchitis* shares its rocky habitats with red raspberry, wild comfrey, herb Robert, and catnip.

On the high crest above Percé in Gaspé, *Saxifraga aizoon* grows with shrubby cinquefoil, yarrow, buffalo berry, harebell, tall buttercup, and red raspberry.

Rubus parviflorus, one of the species which draws botanists from afar to the Keweenaw Peninsula, there competes for its habitat with oxeye daisy, wild strawberry, pearly everlasting, white heath aster, timothy, dandelion, and bracken.

Near Eagle Harbor, Keweenaw, I found burdock growing with *Adeno-caulon bicolor* on the flood plain of a brook.

In their enthusiasm for rarities, botanists are prone to overlook the common species associated with the rare and their occurrence is seldom recorded in the literature. Conditions like those cited are, however, not exceptional. Rather, they are generally encountered.

These common species associated with the rarities are regular invaders of fields wherever the intermission of cultivation gives them a chance. They owe their present abundance largely to man's activity in opening habitats for them. In the primeval forest they are confined, with the rarities, to the unfavorable habitats where the species of the climax forest cannot follow. Many of them were originally as scarce as the species which are rare with us. The difference is that those that are still rare do not spread fast enough to take advantage of man's clearings. For example, in the Sugar Grove District of Ohio common ragweed was found growing in the miniature tundras at the top of the cliffs along with reindeer moss (Griggs 1914, p. 278). It does not occur elsewhere in the untouched vegetation of the region and before man came upon the scene must have been scarce.

The fact that such species are pestiferous weeds in cleared land is apt to give a false idea of their competitive capacity. It is only where man makes and keeps a place for them that they can maintain an abundance. When a field is allowed to revert to forest they are soon eliminated by other species, so revealing their real incompetence in the struggle for existence.

Thus we are brought to the seeming paradox of putting the commonest of plants, the ubiquitous weeds, into the same category as the rarest. Nevertheless, reflection will show that the similarities are fundamental and illuminating. The similarity lies in the fact that life for both is individually pre-

carious because of lack of capacity to compete with the climax vegetation. The presence of burdock side by side with the extremely rare *Adenocaulon bicolor,* noted above, indicates that the ground in the shaded flood plain where they grew, despite its stand of forest trees, was an unstable habitat.

LACK OF COMPETITIVE "AGGRESSIVENESS" IN
EASTERN RARE PLANTS

Most writers who have discussed the rare plants of the St. Lawrence basin have commented on their lack of competitive "aggressiveness" in contrast with the members of the Canadian Flora which hem them in. Marie-Victorin (1929, p. 73) speaking somewhat figuratively of the rare western plants in Quebec says: "A law of death seems to pursue this cordilleran floral element, a law which reduces it to hide in protected ravines to escape the destruction which finally awaits it."

UNAGGRESSIVE RARE PLANTS THRIVE IN A GARDEN

Nevertheless when Marie-Victorin brought some of these same species into the garden, "Quite unexpectedly they are very successful. *Aster gaspensis* spreads rapidly through its underground system. *Erigeron compositus* is selfsown and tends to become weedy on the artificial limestone beds. *Cirsium minganense* has germinated and enjoys the Montreal climate. *Arnica chionapappa*[3] is overgrown and produces tremendously numerous and vigorous rosettes. *Solidago multiradiata,* which in my·personal experience at Cap Gaspé has not spread outside its narrow cornice for the last fifteen years, here behaves as aggressively as any other goldenrod. *Antennaria gaspensis* and *Antennaria rupicola* override their assigned places and flow on all sides in dense mats" (Marie-Victorin 1938, p. 553). The difference between these plants in garden plantings and in the wild is clearly that weeds are not allowed to choke them in the garden.

RARE PLANTS COMMONLY GREGARIOUS

Recognition that rare plants most frequently occur in unstable, pioneer habitats where competition with other plants is reduced to a minimum carries us a good way toward an understanding of rarity but falls short of meeting the whole problem. Cliffs and river gravels are to be found everywhere, but only in certain areas do such habitats carry many rare plants— otherwise they would be no longer rare. One of the most remarkable things about rare plants is the fact alluded to in the first paragraph—that they are commonly concentrated in special districts which are famous for their rarities. From this concentration of rarities, many have been led to believe

[3] Frère Marie-Victorin informs me personally that this should have been written *A. mollis.*

that habitats with numerous rarities must have some physical peculiarity especially suitable for the plants that grow nowhere else in the region.

In a few cases special fitness may be readily demonstrated. The well-known occurrence of maritime plants, which are certainly rare enough in the interior, at the salt works at Syracuse, New York, immediately comes to mind.

But in most localities noted for their rare plants, it is difficult to make out such special fitness. There has been much speculation in the effort to discover some physical peculiarity of soil or climate to these areas. At first sight, it may seem as though special fitness of some sort is required to maintain species that cannot grow elsewhere. But more careful consideration will show that such a conclusion is by no means necessary. Rare plants of diverse habitat preference are commonly found together.

It should be pointed out that the rare plants of the salt springs differ radically in character from those of such areas as Sugar Grove, Ohio, or Bruce County, Ontario. All of the saline rarities are halophytes but most areas with a high concentration of rarities harbor species of diverse ecologic and geographic affinity.

RARE PLANTS OF DIVERSE GEOGRAPHICAL AFFINITY
CONGREGATE TOGETHER

Into the Sugar Grove district, for example, stretch *Betula lutea, Lycopodium clavatum, L. inundatum, Melampyrum lineare,* and *Viola rotundifolia* from the north; *Aster linarifolius, Phlox stolonifera, Rhododendron calendulaceum, Silene rotunifolia, Trichomanes boschianum* from the south; *Sullivantia Sullivantii* from the west; *Lygodium palmatum, Clintonia umbellulata, Eupatorium rotundifolium, E. aromaticum, Phacelia dubia, Rhododendron maximum* from the east (Griggs 1913; Transeau and Williams 1929; Schaffner 1935, 1938). Though many of these are the commonest of plants in other regions, like the devil club on the west coast, all are rare in Ohio. These species occur, moreover, in diverse habitats: *Betula lutea, Phlox stolonifera, Rhododendron maximum, R. calendulaceum,* and *Clintonia* in deep, cool, densely wooded ravines; *Lycopodium* and *Phacelia,* on rocks periodically desiccated; *Sullivantia,* on dripping cliffs; *Melampyrum* in dry upland woods; *Viola* on rather dry sandy talus; *Silene* on the floor of dry sandy rock shelters; the *Aster* and the *Eupatoriums* in old fields.

Not only do the rare species found in such refuge areas usually grow in varied habitats within the special areas; often species ordinarily occurring in diverse habitats grow side by side in the localities where they are rarest. It was anomalous behavior of this sort that was recorded by Stebbins in the passage quoted on page 577, listing the remarkable mixture of

northern, southern, oxyphile, and basiphile plants growing together on the Bruce Peninsula.

The diversity of characteristics which would have to be attributed to a single habitat to explain situations like this on the Bruce Peninsula almost reduces the theory of special fitness to an absurdity. It would seem to compel us to suppose that the same habitat was especially cool to accommodate the northern species and especially warm to protect the southern—not to insist that it be at once acid and alkaline!

RANGES OF RARE PLANTS OFTEN DISRUPTED

One striking feature of rare plants mentioned several times above and repeatedly emphasized by Fernald and Marie-Victorin is the fact that many rare plants are outliers separated by distances of hundreds or thousands of miles from their relatives, these being sometimes identical and sometimes varietally or specifically different. Such disrupted areas are interpreted as relicts of ranges once continuous, and the interpretations have been confirmed in many cases by fossils. Disrupted ranges are, therefore, evidence of races slowly disappearing before the competition of types more fit.

That the rare species are in fact slowly approaching extinction is implied by the comments of nearly all who have observed them. Marie-Victorin's opinion has already been quoted (page 584). Fernald and others repeatedly speak of their ''conservatism'' and lack of ''aggressiveness'' in contrast with the common plants.

This lack of aggressiveness and the disrupted ranges of rare plants fit together perfectly with their restriction to habitats where the common dominants cannot follow and complete the picture of competitive incompetence outlined in the beginning as the fundamental cause of rarity.

SURVIVAL OF RARE PLANTS ATTRIBUTED TO
PLEISTOCENE NUNATAKS

Recognizing the lack of aggressiveness of the western plants that are rare in the east and reasoning from the manifest antiquity of their disrupted ranges, Fernald (1925, 1935, and other papers) supposed that such plants are preglacial or, in his later papers, pre-Wisconsin relicts which owe their presence in the east to preservation on some area that was not only free of ice but climatically suitable for these species through the period of glaciation. This nunatak hypothesis was suggested by the fact that the Gaspé Peninsula, which as has been seen is one of the most notable refuges of rare plants, was never overridden by the continental glacier, but bore only ''local glaciers from the Shickshock Mountains'' which left very little evidence of their presence so that ''it is mainly the scattered stones derived from the

mountains that prove that ice once covered the lower ground" (Fernald 1925, p. 298).

The manifest similarity in the mode of occurrence of the rare species in other areas which were indubitably covered with ice promptly led to an expansion of the nunatak hypothesis to include migrations from supposed nunataks into the present refuges. The Mingan Islands, whose rarities have been repeatedly referred to above, were certainly first scoured by the continental ice, as is shown by grooves, striae, and erratics, and then, at the close of Wisconsin time, submerged for a long period under the waters of the Champlain Sea, whose marine fossils are found on Anticosti and the adjacent mainland at levels far above the highest of the Mingans.

With the recognition that the flora of areas submerged in late Wisconsin times must be postglacial it was supposed that such areas must have been colonized from some nearby nunatak.

But whether one believes with Fernald (1925, p. 314) and Marie-Victorin (1938, p. 543) in migration from such hypothetical nunataks or disbelieves with Wynne-Edwards (1937), the problem of accounting for the occurrence of these plants remains the same.

PROBLEM OF RARE PLANTS THEIR PRESENT PERSISTENCE, NOT THEIR PAST DISPERSAL

The problem of rare plants is to account for their present concentration in special refuges—not to ascertain where or how they endured the several glaciations. If we possessed certain and unquestioned knowledge of the distribution of these species during the Pleistocene, that understanding could give only minor aid in explaining their present limitations.

If we suppose that it is agreed that the rarities of the Mingan Islands, for example, had persisted through the Wisconsin ice age on a nearby nunatak, either the summits of the Laurentides as thought possible by Marie-Victorin or the mountains of Newfoundland as suggested by Fernald, the problem is to ascertain why, of all the possible areas near that nunatak which their disseminules must have reached in postglacial time, this one alone supplied conditions in which they succeeded in establishing themselves.

That we have to deal with a problem of colonization rather than of dispersal will be seen at once when it is considered "that the Mingania thistle like all thistles produces every year thousands of plumed seeds, scattered landward by the strong breezes of the Gulf. Why then is this plant so restricted in its distribution? Why is it apparently dying away? And this is indeed no exceptional case. . . . The light and mobile plumed fruits of *Dryas Drummondii* do not seem to be instrumental in extending its distribution" (Marie-Victorin 1938, p. 541). "The endemic *Taraxacum laurentianum,* a sturdy dandelion of the gravel bars of Mingania, Anticosti,

and western Newfoundland, sends out its seeds in the same fashion as the ubiquitous plant we all know but the endemic plant has nevertheless a very restricted distribution'' (Marie-Victorin 1938, p. 553).

The high percentage of ferns among the rare plants is clear testimony that it is persistence rather than dispersal which must be explained. The wind-borne spores of ferns are carried hundreds of miles with the greatest ease—witness the occurrence of the subtropical *Adiantum Capillus-veneris* at a hot spring in South Dakota. Undoubtedly the spores of this species have fallen generally throughout the territory between the main body of the range and this distant outpost but only where the climate was locally mitigated by the hot water could the species gain a foothold.

This point is strongly emphasized by Cockayne in his consideration of the origin of the New Zealand flora (1928, page 419) :

''Regarding the seed plants, the important evidence already given concerning the distribution of alien species in New Zealand, equipped in every way for travel and ecesis, and their relation to the primeval vegetation, shows how exceedingly difficult it is for a plant to gain entrance into a virgin plant-formation, also it has been seen of how slight advantage for long-distance travel is the possession of flying apparatus or of fruits palatable for birds, and how it is *not* the *species* which move but the *associations* to which they belong. Even absolutely bare ground perfectly suitable as a seed-bed, is only occupied by species from the immediate vicinity, as in the case of the new ground after the Tarawera eruption, river-beds with their seed-catching mat plants, ground left bare by retreating glaciers and many ideal places for seed-germination made by the operations of man.

''Ecesis, rather than the possibility of bird-carriage, etc. during long periods of time, is the great stumbling-block. . . . All these facts and others of a like kind could be cited, showing how seeds could be *rapidly* conveyed over great distances, but, *between the arrival of seed or spore and its becoming a mature plant in a situation favourable, not only for its well-being, but for its increase, is altogether another matter.*''[4]

The problem of the Laurentian rare plants is not how they reached their present areas, but why they have persisted there and nowhere else.

The reason must perforce lie in some peculiarity of the refuges themselves. As has been seen already, attempts to discover some special physico-chemical fitness in these stations have not met with success, and I have nothing to add in this line. As I visited one after another of these places, however, certain features which they possess in common began to be manifest. As has been already detailed, it became clear that most of the rare plants are confined to habitats ecologically young. But pioneer habitats occur everywhere; it is only in very special places that they support any number of rare plants. Evidently the answer must lie deeper than this.

[4] Italics in original.

WHY SO MANY RARE PLANTS IN THE ST. LAWRENCE BASIN?

If the plants rare within the glacial border are considered separately from those rare beyond it and their occurrence is plotted, it is at once apparent that the number confined to the shores of the St. Lawrence drainage system is far greater than would be expected from its relative area. Why? Further, it is a surprising fact, but it is a fact, that most of the districts known to harbor numerous rarities are either islands or peninsulas.

The islands include:

Anticosti, harboring	*Habenaria unalascensis*[5]
Cape Breton Island	*Goodyeria decipiens*
Fishing Islands, Bruce Co.	*Habenaria unalascensis*
Flower Pot Island, Bruce Co.	*Asplenium cryptolepsis*
Great Cloche Island	*Habenaria unalascensis*
Isle Royale	Devil Club, *Oplopanax*
Magdalene Islands	*Potomogeton filiformis* var. *Macounii*
Mingan Islands	*Arctostaphylos rubra*
Newfoundland	*Hordeum boreale*
Prince Edward Island	*Aster laurentianus*
Slate Islands, L. Superior	*Dryas Drummondii*

The peninsulas are:

Bruce	*Phyllitis scolopendrium*
Cloche	*Cypripedium arietinum*
Gaspé	*Polystichum mohroides*
Keweenaw	*Ceanothus sanguineus*
White Fish Point, L. Superior	*Vaccinium membranaceum*

Is the concentration of rarities on islands and peninsulas an accidental coincidence or is it a significant fact? The mathematical chances against coincidence are very great indeed. But if significant, what is the significance? It will be agreed that insularity is to some extent a barrier to plant colonization. Is it possible that in these refuges the ecological succession has been held back just enough ·by mere isolation to have saved the rare species from the elimination which has overtaken them elsewhere?

So far as the dissemination of seed is concerned the obstacle presented by a peninsula is inconsequential. But when the case is examined in the light of what little we actually know of plant migration and succession it will not be dismissed without careful consideration. Colonization of bare ground such as that vacated by a glacier proceeds rapidly, but migration of a plant association into competing vegetation is slow. The spruce trees at Kodiak, for example, mature seeds in enormous quantities and they are carried far and wide by the wind, yet so few of them succeed in gaining a foothold in grassland beyond the woods that the forest, far from sweeping forward

[5] I mention a single rare species in each locality. In most cases a full citation would include a long list, but there is no need here of more than illustrating the point.

across the country climatically suitable for trees, makes a net advance as shown by ring counts of only a mile a century (Griggs 1934b)—this in a region where plant migration is exceptionally rapid.

The reciprocal side of this situation is presented by the rare plants, which, as is well known, are often abundant in the stations where they are established and there succeed in holding, or almost holding, their ground. Although they can by no means extend their boundaries and are evidently giving way under competition with the dominant vegetation, as has been commonly noted by careful observers, yet their retreat is so slow that it cannot be detected over any short period of years.

RARE PLANTS ON YOUNG LANDS

But while one may well be disposed to doubt whether the slight degree of isolation possible to the rare-plant refuges of the St. Lawrence Basin can be significant under the present geographical relations, many of these refuges have undergone great changes in physical condition which appear to have had a critical effect on their present flora.

The Bruce Peninsula of Ontario to which reference has been repeatedly made contains one of the most notable assemblages of rare plants that remain to us, including, in addition to those already mentioned: *Pellaea atropurpurea, Thelypteris Filix-mas, Rubus parviflorus, Adenocaulon bicolor,* and half a hundred other notable rarities. This peninsula was first overrun by the late Wisconsin ice, which has left evidences of its presence in frequent unweathered erratic boulders. Then, after the ice retreated, the land was washed by the waters of glacial Lake Algonquin at many levels (Stanley 1937). The greater part of the present peninsula long stood as a series of reefs covered with shallow water whose waves carried away the glacial till and soil leaving large areas of rock which remain bare of soil to this day. The very area noted above, on which Stebbins recorded northern and southern, calciphile and oxyphile plants, is a bare pavement which is exactly characterized by Fernald's (1935, p. 204) description of Cloche Peninsula a few miles further north across the strait, at the opposite entrance to the Georgian Bay: "The lowermost levels of Cloche Peninsula and of Great Cloche Island are very flat and obviously only recently emerged from the lake. Their scoured and washed surface is a limestone pavement, often of a beautifully regular cancellate pattern." Yet on this particular area he found two of the rarest of plants, *Habenaria unalascensis* and *Cypripedium arietinum.* But its more common and characteristic vegetation as I have observed it consists of such weeds as *Ambrosia artemisiifolia, Potentilla fruticosa, P. anserina, Achillea millefolium,* and *Prunella vulgaris.*

Not only were the Bruce and Cloche Peninsulas no refuges where preglacial plants could have persisted through the glacial cataclysm, they were

actually unready for any plant colonists for long centuries after adjacent areas began to recover from the glacial denudation,

Far from being an obstacle to the understanding of the rarities of the district, recent emergence from the lake is, I believe, the key to it.

The Keweenaw Peninsula which has an even more numerous and more remarkable assemblage of rare plants, largely of western distribution, has had a very similar history. After being covered several hundred feet deep by the late Wisconsin glacier (Bergquist 1937), it was submerged, all but a very small island 32 feet high and perhaps an acre in extent, under the waters of Lake Duluth (Leverett 1929). The duration of Lake Duluth has not been worked out in detail, but is to be measured in centuries rather than in shorter units (Leverett in lit.). The vegetation of the Keweenaw Peninsula also is therefore younger than that of the adjacent mainland.

From evidence entirely similar it is clear that the Mingan Islands first became available habitats for plants upon the recession of the Champlain Sea many centuries after the adjacent mainland of the north shore was bare.

The apparent preference of rare species for districts where the vegetation is demonstrated by geological evidence to be younger than in the surrounding areas barren of rarities fits in with the preference of these species for habitats ecologically young. If this is correct, it is to be expected that with increasing maturity of the vegetation they will be eliminated from these last refuges as many of them have been throughout the large areas between their present stations and the main bodies of their ranges.

The very remarkable localization of the refuges of rare plants on the shores of bodies of water in the St. Lawrence system, a localization several times greater than could be accounted for by the natural prevalence of pioneer habitats near the shore, would find its explanation on this basis. For because of the several predecessors of the present Great Lakes there have been more post-Wisconsin changes in geographical distribution of land and water in this basin than anywhere else in North America. The correlation between the distribution of rare plants and postglacial submergences is too good to be accidental.

Up to this point our thesis is supported by a considerable body of demonstrated fact. The data used have been drawn largely from the work of others better acquainted than the writer with the occurrence of these rare plants. Our contribution has been merely to confirm these data by our own field work and to present them from a new point of view. I should now mention some related problems not solved by the considerations here developed which will have to be met before our hypothesis could become generally useful.

Why is it that many of the plants which are rare in eastern America are common in the west? Our thesis would lead to the conclusion that competitive conditions must be easier in the west. There is at present no understanding

of competition sufficient to permit an approach to this question. Whatever answer might be found a comparative study of competitive conditions east and west would be of the utmost value.

Our thesis explains several of the refuges of rare plants in the St. Lawrence basin. What of the others? Certainly an understanding of the occurrence of rarities in the Bruce Peninsula indicates the desirability of restudy of other refuges like Gaspé, Bic, and Newfoundland where the simple thesis here propounded does not appear to apply. The advisability of restudy of Gaspé, for instance, is emphasized by the fact that clearly emerges from the literature: that, whatever the age of the oldest vegetation, the large majority of the rare plants are confined to new and unstable habitats.

Further, one asks about other famous refuges for rare plants such as the Sugar Grove country, the pine barrens of New Jersey, the southern Appalachians, or the valleys of California, all of which lie beyond the glacial border and have certainly been continuously available for plant habitation over a very long period. Preliminary study indicates that the hypothesis here applied in specific terms to some of the Laurentian areas if recast in more general form may explain the concentration of rarities in some of these older areas also. If the hypothesis is stated in terms of comparative stages in ecological succession rather than in comparative actual ages in years, the rugged hills of Sugar Grove and the sands of the pine barrens will be seen to fit into the same frame of ecological youth as the limestone barrens of Bruce. Study of competitive conditions in other rare plant refuges will be most profitable.

<div align="center">SUMMARY</div>

In conclusion the thesis that has developed from the analysis may be formulated.

1. A species is rare because it cannot compete successfully with the common plants. This is supported by a variety of evidence from different types of data.

2. Most rare species find their habitats in the early stages of the ecological succession. This is supported by citations of many specific cases. The list could be extended indefinitely but exceptions are scarce. This is interpreted as a consequence of point 1.

3. Many rare plants have disrupted ranges. These must once have been continuous. They are therefore slowly dying out. This is held to support point 1.

4. Several areas notable for the large number of rare plants, which they harbor are shown to have been under water long after the retreat of the Wisconsin glacier had opened adjacent areas for plant colonization.

5. It is believed that the rare plants have been eliminated from the older adjacent barren areas by competition with the more competent common

vegetation but persist in the refuges more recently opened to colonization because the ecological succession there has not run quite so far as elsewhere.

6. If the thesis here presented is correct it will be recognized that from it can be worked out improved methods for studying the rate of ecological succession.[6]

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[6] After this article was completed and accepted for publication, Cain (1940) published an interesting paper devoted more specifically than the present paper to the plants of the so-called nunatak areas. He suggests that the apparent senescence of these relict plants may be due to the decreased heterozygosity consequent upon isolation, i.e., that the western wide-ranging relatives of the plants rare in the east are made up of a number of jordanons as contrasted with relatively pure lines in the rare relict types. This would provide a possible answer to a part of the problem specifically left without solution in the present paper, viz.: Why do the western types show greater competitive competency than the eastern? Clearly, eastern and western representatives of these species should be compared as closely as possible. Cross transplantation, interchanging eastern and western relatives, would certainly prove worth while.

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A NEW CUPULE FROM THE LOWER CARBONIFEROUS OF SCOTLAND

HENRY N. ANDREWS

(WITH THREE FIGURES)

While collecting fossil plants in the oil shales near Broxburn, West Lothian, Scotland, in 1938 the author was fortunate enough to obtain a remarkably well preserved fructification, presumably a pteridosperm cupule,[1] which is not referable to any described genus.

When discovered it was already partially weathered out from the shale, and when the remainder of the covering matrix was removed with the aid of steel needles the entire cupule stood revealed as shown in figure 1.

It is a large tulip-shaped structure consisting of six lobes which are fused below the point c. The tips of five of the lobes are readily discernible in the photo; the sixth is nearly hidden by the overlying lobe a. The total length of the fossil is 6.2 cm. and the maximum width 2.3 cm. Since all the lobes are nearly alike in size and form there is no reason to believe that it was not radially symmetrical. The actual greatest diameter in life was probably slightly less than 2 cm. The length of the free portions of the lobes varies from 4.1 to 4.4 cm.; the slight variation may be accounted for by erosion of the extreme tips which had been exposed by natural weathering.

The concave appearance is due to compression of the two lobes seen in face view and to the two corresponding ones beneath, a detail which strongly suggests that the contents of the cupule, whether seeds or sporangia, were lost before it was deposited.

The free lobes are thick and almost leathery even in the fossilized condition, and in view of the nature of their finer structure (described below) it seems most likely that they were fibrous or woody in life. The two lateral lobes appear as raised rims. That the original thickness was considerable is further attested by the projecting flanges which may be seen at d projecting somewhat over one millimeter on either side of the fossil and gradually tapering toward the apex of the lobes as the corresponding tangential dimensions of the latter decrease. Since the two lobes seen in face view show no indication of the existence of such a flange its presence may be accounted for by lateral compression at the time of fossilization.

The surface detail of the cupule presents one of its most interesting features. From point d upwards the surface is characterized by a network which stands out sharply in relief when viewed with a binocular lens and is

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[1] The following definition of this structure is slightly modified from Oliver and Salisbury (1911, p. 47): a free sheathing, usually lobed, structure arising from the peduncle and investing one or more seeds.
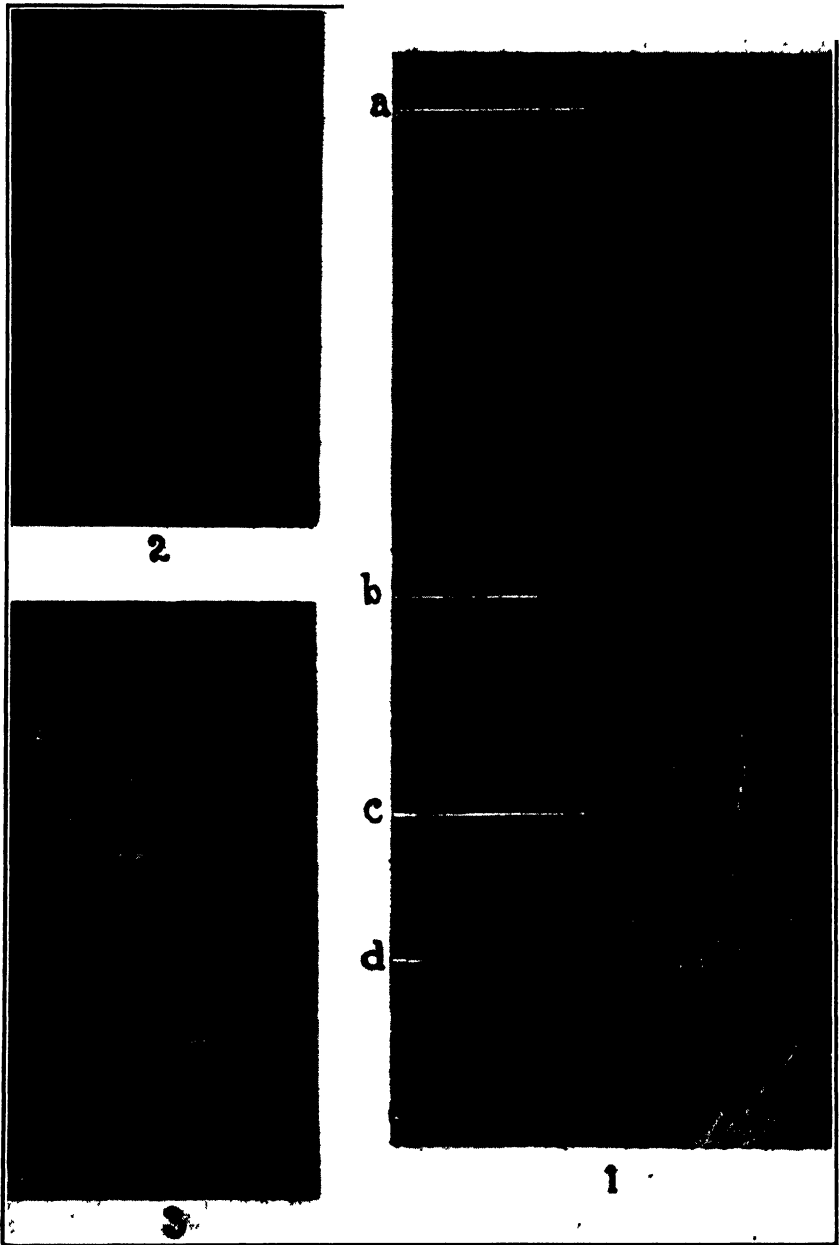
FIG. 1. *Megatheca Thomasii* Andrews. The cupule enlarged × 2.2.

FIG. 2. Surface details of the cupule at *b*, fig. 1. × 40.

FIG. 3. Hypodermal reticulations shown at *c*, fig. 1. × 40.

jet-black in color. It may even be seen with the naked eye in the region around c. Figure 3 presents a magnified portion of this area.

As we proceed towards the apex the number of interstices in the reticulum becomes fewer, until at about the point b they are quite lacking, the surface there being homogeneous or nearly so (fig. 2). Likewise the reticulations are lost below point d, the basal disk of the cupule having a continuous black surface.

If we return now to figure 3, the lack of any discernible structure in the light grayish, oval areas between the meshes of the black network seems to indicate that they were originally occupied by parenchyma which has decayed leaving no trace of cellular detail. The black network, on the other hand, may be seen to have a still finer reticulate appearance (figs. 2 and 3). This secondary reticulation extends to within a few millimeters of the tips of the lobes where it is obliterated by weathering.

The most likely explanation of the major network is that it represents a hypodermal sclerenchyma or mechanical tissue of the so-called "Dictyoxylon" type. Such an arrangement of resistant sclerenchyma and delicate parenchyma might well produce this appearance. The dense black color of the fossil may be attributed in part to absorption of oil, which is so abundant in the shale. It seems probable that the finer or secondary reticulations of the major network represent the outlines (walls) of the cells that originally composed it.

Since the closely compressed lobes shown in face view give no evidence of the presence of any bodies within the cupule it has not seemed advisable to risk destroying the specimen by removing one or more of the overlying lobes.

Megatheca Thomasii Andrews, gen. et sp. nov. Large, deeply lobed, tulip-shaped structure, 6.2 cm. long, 2.3 cm. wide; lobes 6, length of free portion 4.5 cm.; pedicel centrally attached; surface of lower region of lobes reticulate, presumably because of hypodermal mechanical tissue; surface of upper portion of lobes and base of cupule uniform.

Locality: "Roman Camp" shale heap; Broxburn, West Lothian, Scotland. Horizon: Oil Shale Group, Calciferous Sandstone Series. Age: Lower Carboniferous.

The only described structure which may be congeneric with the present specimen is *Calathiops Renieri* Walton from the Lower Carboniferous of North Wales (Walton 1931). The somewhat poorer preservation of the latter does not allow of close comparison and since it is clear that *Megatheca* differs widely from the Permian structure for which Goeppert introduced the name *Calathiops* the new generic name *Megatheca* is proposed.

The cupular nature of *Megatheca* may be called into question. Yet if it is compared with certain undoubted Carboniferous cupules the assumption

is justified. It does possess certain features common to other cupules which allow comparison.

The fructification described as *Calathiops Bernhardti* by Miss Benson (1935) deserves particular attention. In this species the cupules reached a length of 32 mm., which is relatively long when compared with those associated with Upper Carboniferous pteridosperm seeds. According to Miss Benson the cupulate ovules "when immature, are crowded together on the more or less sympodially produced ultimate arms" so that the aggregate appearance of a single group is at first glance not unlike that of *Megatheca* if the size difference be disregarded.

There is a similarity to *Calymmatotheca Kidstoni* Calder in the presence of hypodermal mechanical tissue, the significance of which will be considered on a later page. Professor Walton has kindly informed me of certain semi-petrified fructifications from the Lower Carboniferous of Scotland which he is at present investigating. They are briefly mentioned since they are known to contain a number of stalked seeds (or sporangia?) and are similar in size and form to *Megatheca*. Further comparison must await the completion of Professor Walton's researches; however, this close similarity presents a forceful indication that *Megatheca* was a seed-bearing or sporangia-bearing cupule.

AFFINITIES OF THE FOSSIL

Fronds of *Telangium affine* (L. & H.) constitute the only foliage (other than that of *Lepidophloios scoticus*) associated with *M. Thomasii* and it is therefore quite possible that the latter is the megasporangiate fructification of *T. affine*. In this connection it is particularly notable that Gordon (1938) recently described well preserved remains of stems and petioles under the name *Tetrastichia bupatides,* since there is good evidence in support of his belief that it bore the foliage *Telangium affine.*

It would be of exceptional interest if these fragments, closely associated both in space and time and possessing structural features in common, should be proven to be parts of one plant.

THE MORPHOLOGICAL SIGNIFICANCE OF PALEOZOIC CUPULES

As our knowledge of megasporangiate or seed-bearing fructifications of the Carboniferous accumulates one cannot fail to be impressed by the prominence of the cupule at that time. Its phylogenetic significance must for the present remain debatable, but enough information is available to render justifiable a tentative speculation. To assign it to any of the classical morphological categories is extremely difficult; it can hardly be interpreted as a modification of root, stem, or leaf in the ordinary sense. Its significance as a possible key to the problem of carpel morphology has been considered by Thomas (1936, and earlier papers cited there).

In 1904 Miss Benson put forward a theory that the seed integument is composed of a fused ring of sterilized sporangia, but surprisingly little consideration has since been devoted either to the morphology of the integument or to the cupules which in turn so often enclose the seed (or seeds) of ancient plants.

Miss Benson's hypothesis was based primarily on the clustered synangial nature of the pteridospermic microsporangial sori in general, particularly that of *Heterotheca Grievii*, and also on the structural similarity of such bodies with the integument of *Lagenostoma*.

As far as the integument is concerned it need only be said that more recent investigations of other radiosperms, such as *Physostoma elegans* and *Sphaerostoma ovale*, which likewise possess a more or less segmented integument traversed by a vascular strand in each segment, have brought support to Miss Benson's theory.

The question now arises of a possible common genesis for integument and cupule. Did the cupule perhaps take its origin from a secondary or outer ring of fertile telomes in essentially the same manner as the integument, or from a *secondary outer ring of originally sterile telomes?*

The very large size of *Megatheca Thomasii*, as well as of such cupules as *Calathiops Bernhardti, C. Renieri,* and Walton's undescribed specimens from Scotland, does not harmonize with the supposition that the cupule was derived from sterilized or modified terminal sporangia. Neither does the presence of the apparently sclerenchymatous hypodermal tissues, so clearly shown in figures 2 and 3, suggest a modified sporangium wall. There is, however, a distinct similarity between the hypodermal structure of *Megatheca Thomasii* and the corresponding tissue of the petioles of such pteridosperms as *Lyginopteris, Tetrastichia, Kalymma,* and *Medullosa*.

In attempting to homologize the lobes of these large cupules with telomes one is confronted immediately with the great size of the lobes of *M. Thomasii* as compared with the diminutive terminal segments of the fronds of *Telangium affine*. This divergence in size need not invalidate the general thesis, since neither the frond terminations nor the cupule lobes necessarily represent the original telomic state from which both may possibly have been derived.

In considering the phylogeny of the cupule the following important points should be borne in mind:

1. The cupule is a regular investing structure of Carboniferous seeds of supposed pteridosperm affinity.

2. Cupules from the earlier Paleozoic horizons tend to show a segmented structure, being composed of lobes separate to the base or united below and free above.

3. In cupules in which histological details are evident each individual segment or lobe is supplied with a vascular strand.

4. In certain cupules (*Calymmatotheca Kidstoni* Calder and *Megatheca Thomasii* Andrews) there is a hypodermal mechanical tissue strikingly similar to the hypodermal tissue of the petioles and stems of many pteridosperms.

In the light of our knowledge of pteridosperm microsporangiate fructifications and of such remote psilophytalian forms as *Hedeia corymbosa* Cookson (1935), it is quite possible that a fructification of the ancestors of the pteridosperms consisted of a terminal group of fertile telomes surrounded by a whorl of sterile homologues. The former, aggregating into a synangium and enclosing a single megasporangium, resulted finally in the seed with its single integument. The latter or sterile telomes became flattened and, uniting to a less or greater degree, finally formed the segments of the cupule. If, as is now generally admitted, the pteridosperm frond is a telomic system, this view explains why the subepidermal tissues of the cupule appear so very similar in their general character to the equivalent tissues of pteridosperm petioles and stems.

An attempt to explain the great size of *Megatheca* would at present be premature. It may possibly represent a primitive form which underwent considerable reduction in size in other and later series.

SUMMARY

A cupule from the Lower Carboniferous oil shales of Scotland is described as a new genus, the type species of which is *Megatheca Thomasii*. The cupule is an extraordinarily large (6.2 cm. long) tulip-shaped compression composed of 6 lobes free for two-thirds of their length. Prominent surface reticulations are held to represent the original presence of a "Dictyoxylon" cortex. The fossil was associated with *Telangium affine* (L. & H.).

The hypothesis is put forward that the cupular lobes represent modified (originally sterile) telomes enclosing a group, or groups, of fertile telomes which according to Miss Benson's theory became specialized to form the integument and its enclosed seed.

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PROPAGATION OF HYACINTHUS BY LEAF CUTTINGS[1]

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(WITH EIGHT FIGURES)

It is apparently not generally known that foliage leaves may be used in the propagation of *Hyacinthus orientalis* L. In an extensive review of the propagation of plants by leaf cuttings, Hagemann (1932) includes *H. candicans, H. corymbosus, H. orientalis,* and *H. Pouzolsii.* Stingl (1909) found that two species of *Hyacinthus* would produce roots and bulblets from the base of whole green leaves, or from fractions of one-half or one-third. *H. orientalis* L. formed roots as early as 12 days and continued through a period of 9 weeks. During this time bulblets grew out near the·cut surface on the upper side of the leaf. *H. candicans* Baker developed roots from leaf cuttings after 10 days, and bulblets after 2½ months from 12 of the original 15 cuttings. Histological details were not considered in any of these studies.

When leaf cuttings are placed in moist sand from 2 to 4 weeks many bulblets develop at the basal end. These may be removed as soon as the old leaf decays and serve as a rapid method of propagation. The purpose of the investigation here reported was to determine the origin of these new structures.

METHODS

All cuttings were obtained from *Hyacinthus ·orientalis* L. GERTRUDE grown during the late winter months. The leaves were removed as soon as the flowers were fully opened, and the cuttings placed in clean moist sand. Each cutting consisted of the upper two-thirds of the green leaf. No special treatment was employed. Material was selected for study after 3 days, 7 days, and again after 21 days, killed in chromo-acetic acid, dehydrated in ethyl alcohol, and embedded in paraffin. Longitudinal and transverse sections were made 8 microns in thickness and stained with safranin and Delafield's haematoxylin.

LEAF STRUCTURE

The distal part of the leaf, which is here considered as a portion of the lamina, is flattened and has the linear form typical of many members of the Liliaceae. Stomata are uniformly distributed on both surfaces of the lamina. The vascular strands are arranged parallel to the long axis with numerous minor strands connecting transversely. Internally the mesophyll is composed of large thin-walled cells with no marked differentiation into distinct tissues. Chloroplasts are numerous in all cells except those in the epidermis and near the veins.

DEVELOPMENT OF NEW PARTS

After 21 days approximately half of the original 60 cuttings had developed numerous bulblets. These were found irregularly distributed along the basal edge of the cutting, as shown in figure 1. Occasionally bulblets were found on both surfaces of the leaf, and also several millimeters from the cut surface with no special relation to the main veins. They varied in size from microscopic regions to well rounded structures several millimeters in diameter as shown in figure 1. Apparently their formation is a continuous process which extends over a considerable period of time. The roots originate from within the leaf and appear externally after the bulblet has begun its development.

Initial stages of bulblet formation were found in various epidermal cells near the base of the lamina on the adaxial surface. Cell multiplication becomes evident in several adjoining cells simultaneously, as appears in figures 3 and 4. The first division walls are anticlinal, but periclinal walls soon appear, as is shown in figure 5, and the developing mass of cells becomes externally evident as a raised area on the leaf surface. It is doubtful whether a single cell is responsible for the development of these new parts.

The cells of the epidermis are well differentiated in the normal leaf and exhibit the usual thin peripheral layer of cytoplasm and clearly defined nucleus. When regeneration begins this highly vacuolated protoplasm becomes less vacuolated, the nucleus divides, and a new cell wall appears across the short axis of the cell. Repeated divisions of the nucleus follow, and both anticlinal and periclinal cell walls are rapidly laid down.

Coincidental with this behavior of the epidermal cells meristematic activity starts in one or several layers of subepidermal cells. These cells are all thin-walled and contain many chloroplasts. One of the characteristic features of the first divisions is that many of the newly formed walls extend diagonally, as demonstrated in figure 4. New cell formation continues rapidly; the walls of the original cells may frequently be distinguished after repeated divisions, as is shown in figure 5. Meristematic activity is largely confined to the epidermal and subepidermal cells, but considerable variation may be found in the degree of activity in these two regions, as is evident from a comparison of figures 5 and 7. Sections were sometimes found (fig. 7) in which the epidermis contributed more to the new parts than did other tissues. From groups of these cells scattered over the leaf surface the meristematic masses are formed which soon become organized to produce the new bulblets.

The chloroplasts of the parenchyma cells concerned undergo a change in size and gradually disappear as definitely formed bodies. Measurements of the diameters of chloroplasts from 10 cells taken at random in a fresh
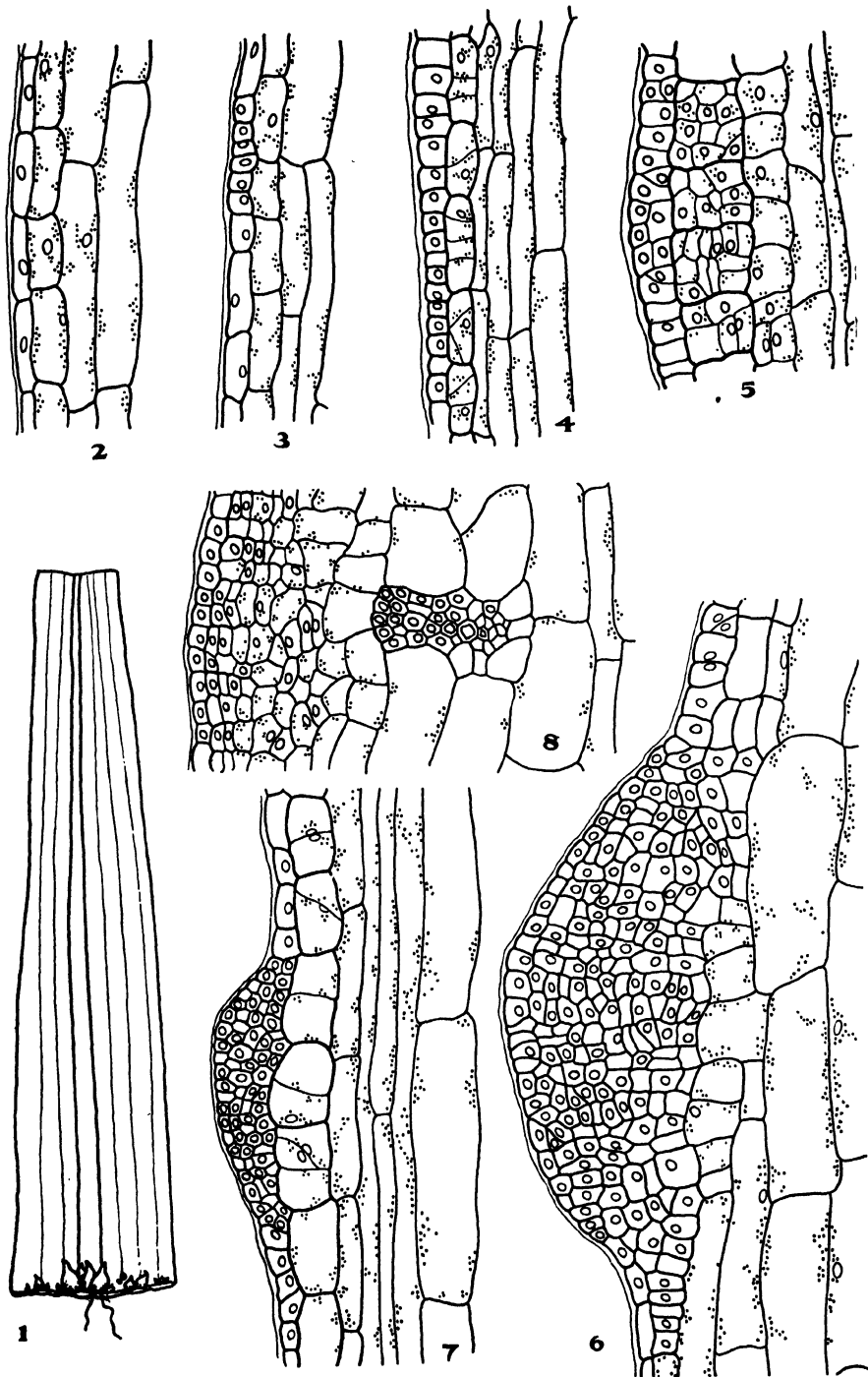
leaf varied from 4.9 to 5.2 microns. Similar measurements made in dividing cells of a regenerating leaf averaged 2.6 microns.

Roots appear externally either from the wounded surface of the lamina, or from the epidermis in close proximity to the young bulblet. They originate from parenchyma cells associated with the vascular system. Figure 8 shows a young root primordium developed from cells near one of the small veins. The root tip soon becomes organized and the new structure emerges through the epidermis. In the sectioned material only one root was found which had been formed directly from the wounded surface. It originated from parenchymatous cells lying next one of the large veins, and extended parallel to the vein until it reached the outside.

<div align="center">DISCUSSION</div>

The histological findings here presented are in agreement with those of Chouard (1933) for *Endymion lingulatus* Chouard (*Scilla lingulata* Poir.). In this species also the bulblets, which were formed on green leaf cuttings, originated by the division of cells of the epidermis and outermost layers of parenchyma. The roots, however, developed from the base of the meristematic mass of cells that formed the bulblet; in *Hyacinthus* the roots originate from cells near the vascular system. Chouard believes that the epidermis of liliaceous bulbs is generally capable of such activity.

Walker (1940) observed that detached scale leaves of *Lilium candidum* and *L. longiflorum* produced bulblets from parenchyma cells near the adaxial surface, and roots from similar cells adjacent to a vascular bundle.

Arber (1925) found histological evidence for meristematic regions in the foliage leaves of *Rhipogonum album* R. Br. when transverse sections were made through the leaf stalk just above its departure from the axis. According to this authority such regions are not uncommon and may be found on both surfaces of the leaf bases of many Monocotyledons. Arber also states that there is often a strong tendency to cell division toward the adaxial surface of leaf bases and petioles, and that this may be one of the factors which has led to bulb formation in some families. In the present investigation leaf bases were not involved and no preformed meristems were

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<div align="center">Explanation of figs. 1–8</div>

FIG. 1. Leaf cutting with bulblets formed after 21 days in moist sand (natural size). FIG. 2. Portion of longitudinal section of normal leaf. FIG. 3. Initial stages of bulblet formation in epidermal cells after 3 days. FIG. 4. Result of meristematic activity in subepidermal cells after 3 days. FIG. 5. The same after 7 days; the original walls of the parenchyma are still discernible. FIG. 6. Internal structure of young bulblet after 21 days. FIG. 7. The result of meristematic activity mostly confined to the epidermis; 7 days. FIG. 8. Root primordium, formed from cells near one of the small veins; 7 days. All except fig. 1, × 100.

found in leaves before they were detached. To what extent this condition may be found in other members of the Liliaceae is now under consideration.

Cook (1930) described briefly the external formation of bulblets near the cut end of green leaves of *Lachenalia* sp., and also stated that *Hyacinthus* and *Narcissus* can be propagated in the same way. I have obtained numerous bulblets on green leaf cuttings of *Lachenalia tricolor* Thunb. placed for one month in moist sand. The histological features of their origin are strikingly similar to those of *Hyacinthus* presented here. Experiments with the green leaves of several varieties of *Tulipa* have given negative results.

The flowering stalks of both *Lachenalia tricolor* Thunb. and *Hyacinthus orientalis* L. GERTRUDE also developed bulblets after 4 weeks in moist sand. These were found along the sides as well as at the ends of the cuttings. Similar results have been reported by Lindemuth (1896) for *Lachenalia luteola* Jacq. and *Hyacinthus orientalis* L.

SUMMARY

Green leaves of *Hyacinthus* form numerous bulblets in moist sand.

The bulblets originate by division of epidermal and sub-epidermal cells.

Roots develop from parenchymatous cells lying near the vascular strands.

There is no evidence of preformed meristematic regions; all new structures are adventitious.

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DESCRIPTIONS OF TROPICAL RUSTS—III[1]

GEORGE B. CUMMINS

(WITH TWO FIGURES)

The Uredinales reported in this paper, with the exception of some few Holway collections, were made available for study through the kindness of Dr. J. R. Johnston and Mr. Paul C. Standley. Aside from the nine new species some other collections of more than usual interest are cited. All types are in the Arthur Herbarium with duplicates of Johnston's collections in the Herbario de la Escuela Nacional Central de Agricultura, Chimaltenango, Guatemala, and of Standley's collections in the Field Museum of Natural History, Chicago, Illinois.

MELAMPSORIDIUM CARPINI (Nees) Diet., on *Carpinus virginiana* var. *guatemalensis* (Winkl.) Macbr. GUATEMALA: Cuesta de las Cañas, above Antigua, Dec. 6, 1938, *Paul C. Standley 58921*.

This species has been reported in North America only from New York.

ANGIOPSORA COMPRESSA Mains, on *Paspalum fasciculatum* Willd. GUATEMALA: near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 63343*.

Only uredia are present in this collection, which appears to be the first record for North America. It is possible, however, that the species has been previously collected and referred to *Puccinia paspalicola* (P. Henn.) Arth.

MAINSIA HOLWAYI Jacks., on *Rubus adenotrichus* Schl. GUATEMALA: near Río Pixcayó, between Chimaltenango and San Martín Jilotepeque, Feb. 3, 1939, *Paul C. Standley 64298*.

I can detect no difference between this and the South American collections. The apically thickened, strongly aculeate urediospores are characteristic. No telia are present.

MAINSIA EPIPHYLLA (Arth.) Jacks., on *Rubus eriocarpus* Liebm. GUATEMALA: slopes of Volcán de Agua, above Santa María de Jesús, Feb. 11, 1939, *Paul C. Standley 65167*.

This species was known previously only from Texas on *Rubus trivialis*. Telia are not present but teliospores present in the uredia agree well, although slightly shorter, $14–21 \times 26–38\,\mu$ as against $13–19(–24) \times 28–45(–48)\,\mu$ in the type.

Cumminsiella Standleyana Cummins, sp. nov. Pycnia et aecia ignota. Uredia hypophylla, subepidermalia, sparsa, cinnamomeo-brunnea, 0.2–0.4 mm. diam.; urediosporae late ellipsoideae vel obovoideae, $18–23 \times 23–29\,\mu$; membrana $2.5–3\,\mu$ cr., flavido- vel cinnamomeo-brunnea, minuteque verru-

cosa; poris germ. 5 vel 6, sparsis. Telia ignota; teliosporae oblongae vel oblongo-ellipsoideae, utrinque rotundatae, medio constrictae, 20–25 × 30–37 μ; membrana 2–3 μ cr., cinnamomeo- vel castaneo-brunnea, verrucosa, quaque cellula poris binis mediis praedita; pedicello hyalino, sporam aequante vel breviore.

On *Berberis fascicularis* (DC.). GUATEMALA—SACATEPÉQUEZ: Slopes of Volcán de Agua, above Santa María de Jesús, Feb. 11, 1939, *Paul C. Standley 65222.*

C. Standleyana is related to *C. sanguinea* (Peck) Arth., but has urediospores with scattered pores and teliospores with shorter and more fragile pedicels.

Ravenelia antiguana Cummins, sp. nov. (Figs. 1, 2.) Pycnia et aecia ignota. Uredia hypophylla, subepidermalia, sparsa, cinnamomeo-brunnea,
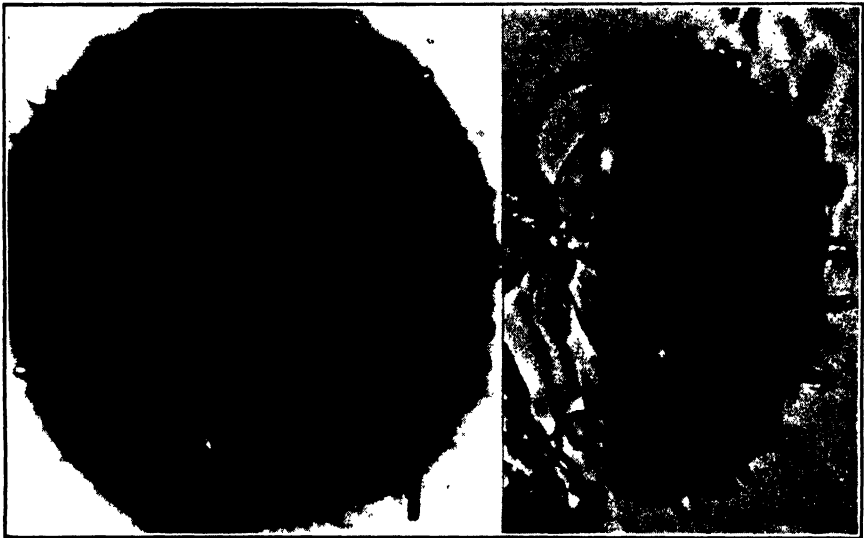
FIG. 1. Teliospore head of *Ravenelia antiguana*, showing the surface sculpture of the spores.
FIG. 2. Lateral view of the same, showing the appressed cysts. × 800.

0.3–0.6 mm. diam.; periphysibus copiosis, capitatis, cinnamomeo-brunneis, 22–25 × 50–70 μ; membrana 1.5–2 μ cr. vel ad apicem 2–3 μ; urediosporae ellipsoideae vel late ellipsoideae, 16–21 × 21–25 μ; membrana aureo-brunnea, 1.5 μ cr., minuteque echinulata; poris germ. 8–10, sparsis. Telia hypophylla, sparsa, subepidermalia, atro-brunnea, 0.1–0.7 mm. diam., paraphysibus nullis vel paucis; capitulis teliosporarum convexis, obscure castaneo-brunneis, 65–115 μ diam., ex sporis 4–6 in omni directione compositis; sporis singulis unicellularibus, 18–27 μ diam., papillis (3–7) subhyalinis 4–8 μ longis obsitis; membrana castaneo-brunnea, 2 μ cr., ad apicem 3 μ; cystidiis eodem numero quo cellulis marginalibus, capitulis adpressis, in aqua in-

tumescentibus et ruptis; pedicello deciduo, ex hyphis paucis composito, hyalino.

On *Cassia biflora* L. GUATEMALA: near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 63356*.

The presence of numerous papillate spines on each teliospore and the possession of appressed cysts, equal in number to the marginal spores, distinguish *R. antiguana* from species previously known to occur on *Cassia*.

Phragmidium guatemalense Cummins, sp. nov. Pycnia et aecia ignota. Uredia subepidermalia, laxe aggregata vel sparsa, praecique hypophylla, flavida, rotundata, 0.2–1.0 mm. diam.; paraphysibus ad marginem paucis, hyalinis, cylindraceis vel clavatis, 7–15 × 45–100 μ; membrana 1 μ; urediosporae obovoideae vel ellipsoideae, 14–18 × 18–27 μ; membrana hyalina vel pallide flavida, 1–1.5 μ cr., minuteque echinulata; poris germ. obscuris. Telia amphigena, inter uredia sparsa, rotundata vel elongata, usque ad 1.5 mm. longa, pulverulenta, atro-brunnea; teliosporae cylindraceae, ad apicem rotundatae vel leniter attenuatae, ex cellulis 3–5 (rarius 1 vel 2) compositae, 19–25 × 43–90(–100) μ; membrana 2.5–3.5 μ cr., obscure castaneo-brunnea, lamina hygroscopica inconspicua, verrucis praesertim parte sporae superiore laxe obsitis; quaque cellula poris germ. 2 vel 3 praedita; pedicello persistenti, hyalino, aequali crassitudine, usque 135 μ longo, 6–9 μ crasso, ad basim rugoso.

On *Potentilla heterosepala* Fritsch. GUATEMALA: Volcán de Agua, Mar. 7, 1916, *E. W. D. Holway 572* (type); Dec. 29, 1916, *E. W. D. Holway 657*, Nov. 12, 1936, *J. R. Johnston 341*; slopes of Volcán de Agua, above Santa María de Jesús, Feb. 11, 1939, *Paul C. Standley 65111*; Tecpám, May 6, 1937, *J. R. Johnston 650*; Cerro de Tecpám, region of Santa Elena, Dec. 26, 1938, *Paul C. Standley 61006*.

P. guatemalense is similar in general to *P. Potentillae* (Pers.) Karst. but is distinct because of the narrower verrucose teliospores. *P. Fragariastri* (DC.) Schroet. has teliospores with similar sculpture but the walls are thinner and lighter colored and the pedicels shorter. The urediospores are verrucose rather than echinulate as in *P. guatemalense*.

Puccinia obtectella Cummins, sp. nov. Pycnia et aecia ignota. Uredia subepidermalia, amphigena, cinnamomeo-brunnea, sparsa, oblonga, 0.6–1.5 mm. longa, diu epidermide tecta; urediosporae ellipsoideae vel obovoideae, 14–18 × 19–26 μ; membrana cinnamomeo- vel flavido-brunnea, 1.5 μ cr., subtiliter echinulata; poris germ. 2, aequatorialibus. Telia amphigena, subepidermalia, multiloculata, indehiscentibus, soris individuis 38–100 μ diam., paraphysibus brunneis coalitis numerosis; teliosporae variabiles, clavatae vel oblongo-clavatae, ad apicem rotundatae vel attenuatae, rarius obtusae vel rostratae, ad basim attenuatae, medio leniter constrictae, 13–19 × 34–60 μ; membrana 1.5 μ cr., ad apicem 3–8 μ cr., castaneo-brunnea, levi; pedicello brunneolo, persistenti, sporam subaequante.

On *Scirpus americanus* Pers. GUATEMALA: near Amatitlán, Dec. 29, 1938, *Paul C. Standley 61342.*

P. obtectella is similar to *P. obtecta* Peck but has significantly smaller spores, especially urediospores, than does the latter. Rarely three-celled teliospores occur.

PUCCINIA FLAVO-VIRENS J. & H., on *Cyperus* sp. GUATEMALA: near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 60297.*

This species was previously known only from Ecuador. The teliospores, characteristically olivaceous under the microscope, may develop in the old uredia or surrounding them. In the latter case the sori are indehiscent, loculate and surrounded by compact, brownish, subepidermal paraphyses.

PUCCINIA PULSATILLAE Kalchbr., on *Ranunculus Hookeri* Schl. GUATEMALA: Las Calderas, Nov. 22, 1938, Dec. 15, 1938, *Paul C. Standley, 57777, 60065;* Oct. 14, 1937, *J. R. Johnston 1464.*

This microcyclic rust has not been reported previously on this host or as occurring south of the United States.

PUCCINIA OBSCURATA Arth. & Holw., on *Neonelsonia ovata* C. & R. GUATEMALA: slopes of Volcán de Acatenango, above Las Calderas, Jan. 3, 1939, *Paul C. Standley 61809.*

Although not so described the teliospores of this collection and of the type are commonly diorchidioid. Pycnia and aecia are also present and a description follows:

Pycnia epiphyllous, few in a group or commonly solitary. Aecia hypophyllous, solitary or 3–5 in a group, short cupulate, 0.3–0.5 mm. in diameter; peridial cells hyaline, coarsely verrucose, ellipsoid or rhomboid, rarely nearly globoid, $20–26 \times 34–45$ μ; aeciospores variable, broadly ellipsoid, ellipsoid, oblong or obovoid, $15–20 \times 22–32$ μ; wall hyaline, 1.5 μ thick, moderately verrucose, the warts often in longitudinal lines.

Puccinia Hackeliae Cummins, sp. nov. Pycniis, aeciis et urediis nullis. Teliis subepidermalibus, praecique hypophyllis, dense aggregatis, maculis leniter incrassatulis usque 5 mm. diam. occupantibus, castaneo-brunneis, loculatis, soris individuis 40–100 μ diam., paraphysibus brunneolis coalitis numerosis; teliosporae 1 (–2–3) septatae, oblongae, clavatae vel cylindraceae, ad apicem obtusae, rotundatae vel conicae, ad basim attenuatae, medio leniter vel non constrictae, $13–18 \times 40–69$ (–80) μ; membrana castaneo-brunnea, 1–1.5 μ cr., ad apicem 3–8 μ, levi; pedicello brunneolo, persistenti, brevi.

On *Hackelia mexicana* (C. & S.) I. M. Johnston. GUATEMALA: locality uncertain, 1938–1939, *J. R. Johnston.*

P. Hackeliae is unquestionably a microcyclic species. The loculate sori with their subepidermal paraphyses are like the telia of *P. rubigo-vera* (DC.) Wint. and perhaps the species can be considered, along with *P. phaceliae*

Syd. & Holw., as correlated with the boraginaceous forms of *P. rubigo-vera.* Unfortunately I have been unable to obtain complete collection data.

Puccinia niveoides Cummins, sp. nov. Pycniis, aeciis, et urediis nullis. Teliis subepidermalibus, flavidis, pulvinatis, compactis, sparsis vel laxe aggregatis, 0.2–1.0 mm. diam.; teliosporae oblongae vel oblongo-fusiformae, utrinque leniter attenuatae vel rotundatae, medio leniter constrictae, 13–16(–18) × (34–)40–46(–50) μ; membrana hyalina vel pallide flavida, 1 μ cr., ad apicem et prope septum 2.5–3.5 μ, levi; pedicello hyalino, sporam aequante. Statim germ.

On *Salvia cinnabarina* M. & G.   GUATEMALA: Volcán de Agua, Nov. 12, 1936, *J. R. Johnston 218*; near San Juan Sacatepéquez, Dec. 8, 1938, *Paul C. Standley 59243* (type).

Previously, three macroscopically similar microcyclic species of *Puccinia* have been described on *Salvia*. All germinate without a rest period. *P. griseola* Lagerh. differs from all in having spores which appear to be sessile and is known only from Ecuador. The relatively common *P. delicatula* (Arth.) Sacc. & Trott. has teliospores with a uniformly thin wall. It has been collected in Mexico and Guatemala. In addition to developing pycnia *P. nivea* Holw. has teliospores which are larger than those of *P. niveoides* but do have the wall thickened apically. It has been collected only in Mexico. *P. niveoides* is intermediate in character between *P. nivea* and *P. delicatula.*

PUCCINIA AMPHIOSPORA (J. & H.) Cumm., on *Hyptis mutabilis* (Rich.) Briq.   GUATEMALA: near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 63851.*

This is the first North American record of the species. It was described on *Hyptis spicata* Poit. from Bolivia.

PUCCINIA INFREQUENS Holw., on *Salvia urica* Epling.   GUATEMALA: Hills of Finca Carmona, southeast of Antigua, Jan. 27, 1939, *Paul C. Standley 63710.*

Pycnia and aecia, present in this collection along with uredia and telia, are described as follows:

Pycnia epiphyllous, few in a group. Aecia hypophyllous, few (2–5) in a group or more extended along the veins, short cylindric, 0.4–0.8 mm. long; peridium brownish, cells oblong, ellipsoid or rectangular, 14–23 × 25–40 μ, finely verrucose; aeciospores ellipsoid or oblong, rarely nearly globoid, 14–18 × 20–26 μ; wall light brownish yellow, 1.5 μ thick, closely and finely verrucose.

PUCCINIA INCONDITA Arth., on *Solanum* sp.   GUATEMALA: slopes of Volcán de Zunil, at and above Aguas Amargas, Feb. 17, 1939, *Paul C. Standley 65336.*

Previously, this microcyclic species was known from three collections, all made in Texas.

PUCCINIA SEORSA J. & H., on *Piptocarpha chontalensis* Baker. GUATE-MALA: near Puerto Barrios, Apr. 25–May 6, 1939, *Paul C. Standley 72528*.

Only aecia are present in this collection. The discovery of telia will be necessary to validate this assignment to a Brazilian species. The aecia are hypophyllous with large coarsely verrucose peridial cells and aeciospores measuring (20–)24–29 × 29–36 µ and with a wall thickness of 1.5–2 µ.

Uromyces antiguanus Cummins, sp. nov. Pycniis et aeciis ignotis. Urediis subepidermalibus, hypophyllis, pallide cinnamomeo-brunneis, laxe aggregatis, 0.5–1.0 mm. diam., vel sparsis et 0.1–0.2 mm. diam.; para-physibus copiosis ad marginem cingentibus, incurvatis, 8–13 × 29–50 µ; membrana hyalina vel flavida, pariete interiore 1–1.5 µ cr., exteriore 2.5–5 µ; urediosporae globoideae vel late ellipsoideae, 17–20 × 19–23 µ; membrana aureo-brunnea vel flavida, 1–1.5 µ cr., minuteque echinulata; poris germ. 8, sparsis vel plus minusve bizonatis. Teliis urediis conformibus sed atro-brunneis, pulverulentis; teliosporae ovoideae vel late ellipsoideae, 19–24 × 23–28 µ; membrana obscure castaneo-brunnea, 2.5–3 µ cr., ad apicem 3–4 µ, moderate verrucosa vel reticulato-verrucosa; pedicello hyalino, usque ad 65 µ longo.

On *Desmodium orbiculare* Schl. GUATEMALA: Cuesta de las Cañas, above Antigua, Dec. 6, 1938, *Paul C. Standley 58900* (type); near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 61735, 63074;* Antigua, Mar. 9, 1916, *E. W. D. Holway 583;* Antigua, July 22, 1936, *J. R. Johnston 779*, July 31, 1936, *J. R. Johnston 76;* Huehuetenango, Jan. 22, 1917, *E. W. D. Holway 761, 764.*

U. antiguanus is related to *U. Hedysari-paniculati* (Schw.) Farl. It is distinct, however, because of the abundant thick-walled paraphyses and the more numerous pores in the urediospores. The teliospores are somewhat more finely sculptured than in *U. hedysari-paniculati,* and the apical wall is thinner and not umbonate.

PUCCINIOSIRA EUPATORII Lagerh., on *Eupatorium* sp. GUATEMALA: Lago de los Pinos, near Sabanetas, Dec. 20, 1938, *Paul C. Standley 60457.*

Arthur (Am. Journ. Bot. **5**: 435. 1918) referred Guatemalan material to this species and later (N. Am. Flora **7**: 700. 1925) reduced the species to synonymy with *Baeodromus Eupatorii* Arth. The Guatemalan specimens were *B. Eupatorii* but Lagerheim's specimen is a *Pucciniosira* and readily distinguishable from *B. Eupatorii.* The present collection appears to be the first from North America.

A redescription of *P. Eupatorii* based upon Standley's collection, which is in excellent condition, follows:

Pycnia not formed. Telia aecidioid, subepidermal, hypophyllous, closely aggregated in groups up to 5 mm. in diameter, columnar, 0.1–0.2 × 0.3–0.5 mm., pale yellowish, with a poorly organized peridium composed of variable, verrucose cells; teliospores 2-celled, oblong or ellipsoid, both ends rounded

or obtuse, slightly or not constricted at the septum which is often oblique or nearly vertical, 16–24 × 26–40 μ; wall hyaline, 1 μ thick, smooth; intercallary cells present, frequently laterally placed.

Uredo antiguensis Cummins, sp. nov. Uredia subepidermalia, hypophylla, flavida, 0.15–0.65 mm. diam., aggregata in maculis brunneis 1–3 mm. diam.; paraphysibus inconspicuis, copiosis ad marginem cingentibus, deorsum coalitis, 7–11 × 20–40 μ, membrana hyalina, 1 μ cr. vel ad apicem leniter incrassata; urediosporae sessiles late ellipsoideae, ellipsoideae vel obovoideae, 14–19 × 19–29 μ; membrana 1 μ cr., hyalina vel pallide flavida, minuteque echinulata; poris germ. obscuris, verisimiliter aequatorialibus.

On *Acalypha guatemalensis* Pax & Hoffm.   GUATEMALA: near Antigua, Nov. 1938–Feb. 1939, *Paul C. Standley 64281.*

This species will perhaps be found to belong in the genus *Phakopsora.*

Peridermium Montezumae Cummins, sp. nov. Pycnia subepidermalia, sparsa, ovoidea, 0.2–0.45 mm. longa, 0.15–0.3 mm. lata, 0.1–0.15 mm. alta, longitudinaliter dehiscentibus. Aecia amphigena, lateraliter compressa, longitudinaliter lacerata, 0.5–1.0 mm. alta, 0.3–1.0 mm. lata, 0.13–0.19 mm. crassa; cellulis peridii oblongis vel oblongo-ellipsoideis, 20–27 × 35–50 μ, pariete interiore moderate verrucoso 3.5–4 μ cr., exteriore levi 1.5–2 μ cr.; aeciosporae late ellipsoideae vel oblongo-ellipsoideae, (20–)23–30 × (28)30–39 μ; membrana hyalina, 5–6.5 μ cr., valde tuberculata, tuberculis rotundatis, cuboideis vel oblongis, 2.5–3.5 μ cr., 2.5–4.5 μ longis.

On *Pinus Montezumae* Lamb.   GUATEMALA: Barranco de los Condenado, May 23, 1937, *J. R. Johnston.*

P. Montezumae resembles *P. guatemalense* Arth. & Kern but has shorter aecia with a more delicate peridium and aeciospores with thicker walls and conspicuously coarser sculpture. The tubercles are rather easily deciduous so that spores partially or completely devoid of them are frequently seen. The inner smooth wall is 2.5–3 μ thick. In *P. guatemalense* the sculpture consists of columnar rods with a length of 3–3.5 μ but a diameter of only 1–1.5 μ.

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A SUGGESTED STARTING–POINT FOR THE NOMENCLATURE OF DIATOMS[1]

RUTH PATRICK

In the study of diatoms it is evident that the date 1753, which is the general starting point for algae, means nothing. It was not until the middle of the nineteenth century, when the perfection of lenses made the critical study of diatoms possible, that accurate descriptions were made. Among the earlier workers such as Ehrenberg, William Smith, and later Pfitzer, Petit, and Mereschkowsky, the classification was based on the morphology of the diatoms. This method was later discarded for one based upon the shape and structure of the dead shell. One of the most important systems of classification based upon the dead shell was that of H. L. Smith, 1872. The main points of his classification were generally adopted in America and in Europe by such important workers as Van Heurck, Mills, De-Toni, Cleve, and others. In 1896 Schütt proposed a system of classification based upon characteristics both of the living plant and of the dead shell. The main principles of this classification are used by most diatomists to-day.

During the nineteenth century a great many papers on diatoms appeared. Many of these were of a floristic nature or records of new and rare species. The first work of any great scope was that of Ehrenberg. However, his descriptions of many species are inadequate or even lacking. Some of his illustrations, though carefully executed, lack detail which is necessary for definite identification. This was, no doubt, partially if not entirely due to defective lenses. The works of such men as Grunow, Kützing, Rabenhorst, and William Smith, though well executed, deal with only a relatively small number of genera. In 1872 appeared H. L. Smith's *Conspectus of the families and genera of the Diatomaceae*. This work gives in the form of a key a fairly complete classification of the genera of diatoms. However, little attention is paid to nomenclature and no detailed descriptions of the genera are given.

During the latter half of the nineteenth century several monographs were published. Important among these are those of Grunow on the families *Epithemieae, Meridioneae, Surirelleae, Amphipleureae, Diatomeae, Entopyleae,* and *Nitzschieae,* of Rattray on the genera *Aulacodiscus, Auliscus,* and *Coscinodiscus,* and of H. L. Smith on the genus *Amphora.*

The vast amount of diatom literature that had been accumulated was not brought together till the publication in 1891 of De-Toni's *Sylloge Algarum,* Volume II, *Bacillarieae.* In this publication we find for the first time practically all genera of diatoms, each with an adequate description. The names of most genera were accurately determined from a nomenclatural standpoint. Though specimens had been cited by a few writers, such as

Rabenhorst and Rattray, previously to this date, this is the first comprehensive work in which we find citations of specimens accompanying the descriptions of species. Until the present time, type specimens and their place of deposition are not usually recorded with the published descriptions of new species.

I propose that 1891, the date of publication of the first part of De-Toni's *Sylloge Algarum*, Volume II, *Bacillarieae*, be the starting point for diatom nomenclature, and that the names of the genera of diatoms published previously to this date and included by De-Toni be considered established as described by him in this work. Though the publication of Volume II of the *Sylloge Algarum* extended from 1891 to 1894, De-Toni did not include all contemporary literature after 1890. Therefore it seems advisable to establish the year 1891 as the publication date for the whole of Volume II.

One generic name, *Surirella* Turp., should be conserved. Turpin named this genus after a Dr. Suriray in 1828. Pfitzer in 1871 stated that if the genus is named after Dr. Suriray it should be *Suriraya*. De-Toni followed Pfitzer's suggestion. According to the International Rules of Botanical Nomenclature, Article 59, *Surirella* Turp. is the valid name. It is also the name used by most workers today.

Of course one must realize that in any such large work there may be mistakes. In De-Toni's work these are mainly in the citation of authorities for names of species. He makes some changes in spelling, but since these changes do not alter the meaning of the original name and since some of them make the names easier to pronounce, I think it wise to adopt his spelling.

Several generic names included by De-Toni are later homonyms of genera in other groups of plants, e.g. *Euodia* Bailey 1861, *Diatoma* DeCandolle 1805, and *Actinella* Lewis 1865. Later names must be adopted in place of these, even if De-Toni is not adopted as a starting-point.

If a starting point such as the suggested one is not established a great many names must be changed, according to the International Rules of Botanical Nomenclature. As has been pointed out by Kuntze in the *Revisio Generum Plantarum*, the following well known generic names would have to be replaced: *Nitzschia* Hassall 1845 by *Homoeocladia* Agardh 1827, *Melosira* Agardh 1824 by *Lysigonium* Link 1820, *Cymatopleura* W. Smith 1851 by *Sphinctocystis* Hassall 1845, *Gyrosigma* Hassall 1845 by *Scalptrum* Corda 1835.

The date of De-Toni's work falls well in line with those already selected for some of the other groups of algae: *Nostocaceae homocysteae*, 1892–93; *Nostocaceae heterocysteae*, 1886–88; *Desmidaceae*, 1848; *Oedogoniaceae*, 1900. Also those generic names previously recommended by H. Peragallo and adopted for conservation at the 1935 International Botanical Congress are not altered by this recommendation.

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA.

STUDIES IN THE AMERICAN CELASTRACEAE—III. NOTES ON MEXICAN AND CENTRAL AMERICAN SPECIES[1]

C. L. LUNDELL

From recent revisionary studies in the Celastraceae, based primarily on material placed at the writer's disposal by the Field Museum of Natural History through the courtesy of Paul C. Standley, four new species are proposed in the genera *Celastrus, Gyminda, Myginda,* and *Zinowiewia.* The obscure *Celastrus mexicanus* DC. and *Dodonaea* (?) *serrulata* DC., both amply represented in the Sessé, Mociño, Castillo and Maldonado collection, are established as valid species of *Wimmeria*; this necessitates the reduction to synonymy of two long recognized names, *W. confusa* Hemsl. and *W. persicifolia* Radlk.[2] A new variety of *Wimmeria microphylla* Radlk., described from the collection of Mociño and his associates, is primarily of interest because it apparently has not been found again in nearly a century and a half of intensive exploration in central Mexico.

Celastrus lenticellatus Lundell, sp. nov. Frutex scandens. Folia petiolata, petiolo 6–12 mm. longo, chartacea, elliptica vel oblongo-elliptica, 10–20 cm. longa, 5–7.8 cm. lata, apice abrupte acuminata, acumine obtuso, basi acutiuscula vel rotundata, serrulata, venis lateralibus 7–9. Inflorescentia multiflora, anguste peniculata, usque ad 13 cm. longa, 4.5 cm. lata. Calyx quinquelobatus, lobis ovatis, 0.5–0.8 mm. longis. Petala 5, oblonga, ca. 1.8 mm. longa. Ovarium liberum, 3-loculare, loculis uniovulatis.

A woody vine, entirely glabrous; branchlets rather slender but apparently quite rigid, densely covered with small raised lenticels. Leaves alternate, exceptionally large. Stipules small, base deltoid, constricted above and filiform-subulate. Petioles short, rather stout, canaliculate, 6–12 mm. long. Leaf blades thin chartaceous, elliptic or oblong-elliptic, 10–20 cm. long, 5–7.8 cm. wide, apex abruptly short acuminate, the acumen obtuse, base acutish or rounded, margin rather remotely serrulate, the teeth not conspicuous, costa slightly raised above, prominent beneath, the main lateral veins 7–9 on each side, plane or slightly impressed above, prominent beneath, secondary veins and veinlets prominulous and reticulate beneath. Inflorescence many-flowered, paniculate, up to 13 cm. long, 4.5 cm. wide, the panicles axillary, usually fasciculate, much-branched to the base, the branches short, slender, crowded. Bractlets ovate-deltoid, acuminate, toothed. Pedicels slender, short, those of buds less than 2 mm. long. Calyx 5-lobed, the lobes ovate, rounded, 0.5–0.8 mm. long, minutely erose. Petals 5, oblong, about 1.8 mm. long, rounded. Stamens 5; filaments about 1.4 mm. long. Disk shallow, about 1.4 mm. in diam. Ovary apparently abortive, free, surrounded at base by disk, 3-celled, with 1 erect ovule in each cell. Style thick, short, truncate.

MEXICO—CHIAPAS: Finca San Cristobal, June, 1914, *C. A. Purpus 7370* (TYPE in the U. S. National Herbarium, no. 567584; duplicate in the Field Museum of Natural History; fragment in the University of Michigan Herbarium).

The species, which has affinity with *C. Liebmannii* Standl., is well-marked by its large strongly veined leaves and exceptionally large many-flowered narrow inflorescences with short branches and pedicels.

The collection was originally distributed as *Perrottetia* (?), and *C. lenticellatus* does bear a superficial resemblance to certain species in that genus.

Gyminda fimbrillata Lundell, sp. nov. Arbor (?) glabra. Folia chartacea, petiolata, petiolo 2–6 mm. longo, oblongo-elliptica vel lanceolata, 2–8.5 cm. longa, 1.2–3.1 cm. lata, apice acuta vel obtusiuscula, basi acuta vel cuneata, crenulato-serrulata. Flores dioecii, ♂ sessiles. Cymae ♂ axillares, multiflorae, ca. 1 cm. longae, breviter pedunculatae. Bracteae fimbrillatae. Sepala 4, ovata, ca. 0.8 mm. longa, fimbrillata. Petala 4, oblonga, usque ad 2.5 mm. longa, 1.2 mm. lata. Stamina 4. Ovarium abortivum. Styli 1.

Branchlets slender, quadrangular at first, slightly sulcate, compressed at the nodes, dark reddish-black. Stipules conspicuous, lanceolate-cuspidate, up to 3 mm. long, reddish, conspicuously fimbriate. Petioles shallowly canaliculate, 2–6 mm. long. Leaf blades chartaceous, drying ashy-gray, oblong-elliptic or lanceolate, 2–8.5 cm. long, 1.2–3.1 cm. wide, apex acute or obtusish, base acute or cuneate, margin crenulate-serrulate, costa slightly elevated on both surfaces, more conspicuous beneath, main lateral veins 7 or 8 on each side, prominulous beneath. Flowers dioecious. Staminate cymes many-flowered, axillary, solitary, rarely exceeding 1 cm. in length including stout peduncle up to 4 mm. long, forked up to 5 times, the branches very short, crowded, the flowers sessile, each node bibracteate, the bractlets deltoid, conspicuously fimbrillate. Calyx 4-parted, the sepals broadly ovate, about 0.8 mm. long, conspicuously fimbrillate. Petals 4, oblong, up to 2.5 mm. long, 1.2 mm. wide, minutely erose. Stamens 4, opposite the sepals; filaments up to 1.4 mm. long, expanded at base into an inconspicuous irregular disk; anthers small. Aborted ovary depressed ovoid, surrounded at base by disk, tapering above into a short simple conical style. Pistillate flowers and fruits unknown.

MEXICO: "Plantae Novae Hispaniae," 1787–1795–1804, *Sessé, Mociño, Castillo & Maldonado 810* (TYPE in the herbarium of the Botanical Garden of Madrid; fragment in the University of Michigan Herbarium). OAXACA: Cafetal Concordia, alt. 800 m., Dec. 25, 1917, *B. P. Reko 3709* (U. S. National Herbarium).

The Reko collection, likewise staminate, differs somewhat in leaf form, but the flowers closely agree with those of the type.

G. fimbrillata is readily distinguished from the other two species in the genus by the simple style of the aborted ovary; the other species have a 2-lobed style. *G. fimbrillata* is marked further by the short many-flowered

staminate cymes, the conspicuously fimbrillate bractlets and sepals, and the poorly developed irregular disk.

Myginda Standleyi Lundell, sp. nov. Frutex. Folia glabra, petiolata, petiolo 2–4 mm. longo, membranacea, anguste lanceolata, 3.5–11 cm. longa, 1–3 cm. lata, apice longe acuminata, basi acuta, serrulata. Inflorescentia cymosa, usque ad 1 cm. longa. Pedicelli usque ad 3.2 mm. longi. Sepala 4, ovata, 0.5–0.7 mm. longa. Petala 4, late ovata vel suborbicularia, usque ad 1.5 mm. longa. Ovarium 2-loculare.

A shrub about 2 m. high. Branchlets very slender, quadrangular, sulcate, glabrous. Stipules filiform-subulate, 0.8–1.5 mm. long. Petioles canaliculate, 2–4 mm. long, glabrous. Leaf blades glabrous, membranaceous, very thin, paler beneath, narrowly lanceolate, 3.5–11 cm. long, 1–3 cm. wide, apex attenuate, long acuminate, base acute, margin serrulate, the teeth obtusish and irregular, costa slightly raised above, prominent beneath, the main lateral veins 5–7 on each side, prominulous and whitened beneath. Inflorescence cymose, axillary, subsessile, solitary but appearing fascicled because of the short peduncle, less than 1 cm. long, the peduncle usually less than 1 mm. long, the primary branches 1.8–2.5 mm. long, the peduncle and branches glabrous; bractlets less than 1 mm. long, bearing few teeth, these red gland-tipped. Flowers 15 or fewer in each inflorescence. Pedicels slender, short, up to 3.2 mm. long (central flower of cyme), usually glabrous, rarely slightly puberulent. Calyx saucer-shaped; sepals 4, ovate, 0.5–0.7 mm. long, minutely erose. Petals 4, apparently purplish, broadly ovate or suborbicular, up to 1.5 mm. long, rounded, slightly erose. Stamens 4, opposite the sepals, inserted in margin of disk, equaling the sepals. Disk quadrangular, flat, about 0.7 mm. in diam. Ovary surrounded by disk, base submerged in torus, 2-celled, with 1 erect ovule in each cell. Style conical, short. Fruits unknown.

GUATEMALA—SAN MARCOS: Finca Vergel, near Rodeo, alt. about 900 m., in wet forest, March 15, 1939, *Paul C. Standley 68938* (TYPE in the University of Michigan Herbarium; duplicate in the Field Museum of Natural History). QUEZALTENANGO: near Calahuaché, alt. about 1020 m., in damp forest, March 1, 1939, *Standley 67130*; Finca Pireneos, below Santa María de Jesús, alt. 1350–1380 m., in dense damp forest, March 11, 1939, *Standley 68323, 68398.*

M. Standleyi is well-marked by its thin narrowly lanceolate acuminate leaves, and small inflorescences less than 1 cm. long.

Wimmeria mexicana (DC.) Lundell, comb. nov. *Celastrus Mexicanus* DC., Prodr., **2**: 8. 1825. *Wimmeria confusa* Hemsl., Diag. Pl. Mex., p. 6. 1878. *W. pallida* Radlk., Sitzungsb., math. phys. Akad. Wiss. München, **8**: 379. 1878. *W. crenata* Liebmann ex Lundell, Contr. Univ. Mich. Herb., **3**: 19, in syn. 1939.

MEXICO: "Plantae Novae Hispaniae," 1787–1795–1844, *Sessé, Mociño, Castillo & Maldonado 5185* (TYPE in the Field Museum of Natural History; duplicate in the University of Michigan Herbarium). Photograph of plate of *Celastrus Mexicanus* DC. from Delessert Herbarium (Field Museum of Natural History, no. 928534; photograph no. 30561).

The copy of the Sessé and Mociño plate upon which De Candolle based his description of *Celastrus Mexicanus* is a poor reproduction of the species. That the original plate was based on *Sessé, Mociño, Castillo & Maldonado 5185* is, however, scarcely questionable. This collection is typical *Wimmeria confusa* Hemsl., and acceptance of the older and more appropriate name is obligatory.

WIMMERIA MICROPHYLLA Radlk. var. **latifolia** Lundell, var. nov. Folia alterna, pilosa, petiolata, petiolo usque ad 3.5 mm. longo, chartacea, obovato-elliptica vel late elliptica, 1.3–3.2 cm. longa, 0.75–1.8 cm. lata, apice acuta, rotundata vel emarginata, basi acuta vel cuneata, obscure serrulata.

Branchlets rigid, striate, at first gray and short-pilose, with age glabrous and reddish. Leaves alternate, appearing fascicled on short reduced branchlets. **Petioles** densely short-pilose, up to 3.5 mm. long. Leaf blades chartaceous, **short** pilose on both surfaces, obovate-elliptic or broadly elliptic, 1.3–3.2 cm. long, 0.75–1.8 cm. wide, apex acute, rounded or slightly emarginate, base acute or cuneate, margin very obscurely serrulate, essentially entire, costa prominulous, slightly elevated beneath, whitened, lateral veins obscure. Cymes with as many as 6 flowers. Flowers and young fruits as in *W. microphylla*.

MEXICO: "Plantae Novae Hispaniae," 1787–1795–1804, *Sessé, Mociño, Castillo & Maldonado 879* (TYPE in the herbarium of the Botanical Garden of Madrid; fragments in the Field Museum of Natural History, and the University of Michigan Herbarium).

In aspect the plant differs considerably from the typical form of *W. microphylla*. Its leaves are wider, either broadly elliptic or obovate-elliptic, and somewhat larger.

W. microphylla var. *latifolia* was reported by Sessé and Mociño under the name "*Celastrus Bullatus*" (Pl. Nov. Hisp., ed. 2, 37. 1893; Fl. Mex., ed. 2, 64. 1894). Their collection bears this name on the original label.

WIMMERIA PUBESCENS Radlk., Sitzungsb. math. phys. Akad. Wiss. München **8**: 378. 1878.

MEXICO: "Plantae Novae Hispaniae," 1787–1795–1804, *Sessé, Mociño, Castillo & Maldonado 906* (in the herbarium of the Botanical Garden of Madrid; fragments in the Field Museum of Natural History, and the University of Michigan Herbarium).

The original label is marked "dudoso."

WIMMERIA SERRULATA (DC.) Radlk., Sitzungsb. math. phys. Akad. Wiss. München **8**: 379. 1878. *Dodonaea (?) serrulata* DC., Prodr. **1**: 617. 1824. *Wimmeria persicifolia* Radlk., Sitzungsb. math. phys. Akad. Wiss. München **8**: 379. 1878.

MEXICO: "Plantae Novae Hispaniae," 1787–1795–1804, *Sessé, Mociño, Castillo & Moldonado 4912* (in the herbarium of the Botanical Garden of Madrid; fragments in the Field Museum of Natural History, and the University of Michigan Herbarium). OAXACA: Ejutla, October, 1842, *F. M. Lieb-*

mann 4044 (TYPE collection of *W. persicifolia* in the University of Michigan Herbarium).

The origin of the specimen upon which De Candolle based the description of his *Dodonaea* (?) *serrulata* has been a source of confusion. The label evidently bears only a locality name "Monte-Video."

The Sessé, Mociño, Castillo and Maldonado collection bears on the original label the name "*Dodonea serrulata*"; hence there is ample justification for interpreting this as the type collection. It is probable that a specimen, inadequately labeled, went to the Thibaud Herbarium, and served as the type for De Candolle.

The original description by De Candolle and the later description by Radlkofer apply satisfactorily in all details to the plant which has been long known as *W. persicifolia*. The type collection of *W. persicifolia* matches the Sessé, Mociño, Castillo and Maldonado specimen exactly. Radlkofer evidently did not see material of *W. serrulata*, for only thus can we account for his redescribing the plant as *W. persicifolia*.

Zinowiewia ovata Lundell, sp. nov. Arbor (?). Folia petiolata, petiolo 6–8 mm. longo, ovata vel ovato-lanceolata, 4–6.5 cm. longa, 2.2–3 cm. lata, apice obtuse acuminata, basi acuta vel subcuneata. Cymae usque ad 3 cm. longae, pedunculatae. Calyx profunde quinquefidus, lobis rotundatis. Petala 5, ovata, usque as 1.5 mm. longa, 1.2 mm. lata. Fructus immaturus samaroideus.

Probably a small tree; branchlets slender, dark red, shallowly sulcate, somewhat compressed at the nodes. Leaves membranaceous and pale yellow-green at first, chartaceous with age and slightly paler beneath. Petioles slender, shallowly canaliculate, 6–8 mm. long. Leaf blades ovate or ovate-lanceolate, 4–6.5 cm. long, 2.2–3 cm. wide, apex short acuminate, the acumen usually obtuse, base acute or subcuneate, costa slightly raised above, prominent beneath, the main lateral veins 4–6 on each side, inconspicuous. Cymes up to 3 cm. long, usually forked 4 times; the peduncle well developed, 6–10 mm. long; bractlets ovate, up to 1 mm. long, bearing red glandular teeth. Flowers apparently pale green, stipitate, the stipe about 1 mm. long. Calyx 5-lobed, the lobes rounded, about 0.4 mm. long, often bearing few minute red deciduous teeth. Petals 5, ovate, up to 1.5 mm. long, 1.2 mm. wide, very minutely erose. Margin of disk slightly raised. Ovary almost completely submerged in disk. Samaras (immature) about 1.7 cm. long, with a broadly oblanceolate-oblong slightly oblique wing up to 0.7 cm. wide, emarginate, 1-celled, 1-seeded, the persistent stipe about 1 mm. long.

PANAMA: vicinity of El Boquete, Chiriquí, alt. 1000–1300 m., March 2–8, 1911, *W. R. Maxon 5109* (TYPE in the University of Michigan Herbarium; duplicate in the Field Museum of Natural History).

The Panama collection, referred tentatively to *Z. costaricensis* Lundell (Bull. Torrey Club **65**: 471–472. 1938; Contr. Univ. Mich. Herb. 3: 43–44. 1939), represents a distinct, but very closely related species.

THE UNIVERSITY OF MICHIGAN
    ANN ARBOR, MICHIGAN

A NEW GENUS AND SPECIES OF STERCULIACEAE

JOSEPH MONACHINO

Veeresia Monachino & Moldenke, gen. nov.

Arbores, foliis simplicibus alternis stipulatis. Inflorescentia terminalis paniculata bracteata. Flores subregulares, calyci clavi-campanulato tandem 4- vel 5-lobato. Corollae petala 4 vel 5 imbricata oblanceolata ungulata 2-auriculata. Filamentorum columna ad apice 5-brevilobata. Antherae ca. 15 sessiles capitatae, loculis diverse dispositis. Staminodia 5. Stigma sessile obtusum obscure 5-lobatum. Ovarium gynophoro longo elevatum obscure 5-lobatum facile per loculum dehiscente, loculis 5, ovulis in cuique locula 2 axilibus minute alveolatis marginatis.

Trees, with simple, alternate, stipulate leaves. Inflorescence terminal, paniculate, bracteate. Flowers subregular. Calyx clavate-campanulate, at first closed, later splitting into 4 or 5 short lobes. Corolla composed of 4 or 5 petals, which are imbricate in bud, oblanceolate, clawed, with 2 very short auricles below the middle. Filament-column 5-lobed at apex, the lobes short. Anthers about 15, sessile, capitate, their cells arranged in diverse positions. Staminodes 5. Stigma sessile, blunt, obscurely 5-lobed. Ovary borne on a long gynophore, obscurely 5-lobed, readily splitting loculicidally, 5-celled. Ovules 2 in each cell, attached to a central placenta, one above the other, flattened, minutely pitted, margined. Fruit not seen.

The genus is apparently a member of the *Sterculiaceae*, tribe *Helictereae* as defined by Bentham & Hooker in Gen. Pl. 1[1]: 215 (1862) and by K. Schumann in Engler & Prantl, Nat. Pflanzenfam. 3[6]: 92 (1895), closely allied to the Asiatic genus *Reevesia*. It differs from *Reevesia*, however, in the presence of staminodes and in other characters, but its final status may depend on an examination of the fruit, which has to date not been collected. The generic name is an anagram of *Reevesia*, whose 3 known species inhabit the eastern Himalayas and China. The following species is to be regarded as the type of the genus.

Veeresia Clarkii Monachino & Moldenke, sp. nov. Arbor magna; hornotinis stellato-pubescentibus; stipulis linearibus 0.5–1 cm. longis caducis dense pubescentibus; petiolis 1.5–4 cm. longis dense pubescentibus; laminis ovatis 4–10 cm. longis, 2.5–8.5 cm. latis, obtusis vel acutiusculis vel breviter acuminatis, integris vel irregulariter dentatis, ad basim cordatis vel rotundatis et palmate 3–5-costatis, supra stellato-pubescentibus, subtus dense stellatis, pilis canescentibus; paniculis multifloris terminalibus axillaribusque canescentibus; bracteis linearibus caducis; pedicellis 1–3 mm. longis; calyce 4–5 mm. longo, 3–4 mm. lato, lobis triangularibus obtusis, extus canescentibus, intus glabris; petalis oblanceolatis vel spathulatis, ca. 11 mm. longis, venosis, extus dense stellato-pubescentibus, intus glabris vel sparse pubescentibus.

A large tree; new twigs rounded, grayish stellate-pubescent; stipules linear, 0.5–1 cm. long, caducous, densely pubescent; petioles roundish in cross-section, 1.5–4 cm. long, densely pubescent; leaf-blades ovate, 4–10 cm. long, 2.5–8.5 cm. wide, varying from blunt to acutish or short-acuminate at

apex, entire to irregularly dentate along the margins, cordate or rounded and palmately 3–5-ribbed at the base, pubescent with distinct stellate hairs above, densely canescent-stellate beneath; primary veins 4–6, distinctly prominulous beneath, curvate, confluent near the leaf-margin; panicles terminal and axillary, many-flowered, canescent, longer than wide; bracts linear, caducous; pedicels 1–3 mm. long; calyx 4–5 mm. long, 3–4 mm. wide, its lobes shorter than the tube, triangular, blunt, canescent outside, glabrous within; petals oblanceolate to spatulate, broadest near the apex, about 11 mm. long, distinctly venose, densely stellate-pubescent outside, glabrous or sparsely pubescent within; staminal tube (synema) about 2 cm. long, shallowly 5-lobed at the apex; ovary pubescent on the sutures, otherwise glabrous; stigma sessile; fruit not seen.

The type of this species is *Ora M. Clark 7401*, collected on mountainsides north of Chapahuacan, Hidalgo, Mexico, 2 July 1935, at an altitude of 8000 feet, and is deposited in the Britton Herbarium at the New York Botanical Garden.

THE NEW YORK BOTANICAL GARDEN
    NEW YORK, NEW YORK

The *Index to American Botanical Literature* has been a feature of the Bulletin of the Torrey Club for nearly 60 years. At first it included 15 or 20 titles in each issue; the articles dealt mainly with taxonomy and floristics. In recent issues the number of titles has increased to over 300, and the articles range from taxonomy to physiology, pathology, and genetics (complete listing of American work, however, has probably never been attained in recent years). Many teachers and investigators have found the *Index* valuable, for titles are listed in it long before they appear in any of the abstract journals.

Criticism of two kinds has recently been directed at the *Index:* (1) Its increased size has increased the financial burden on the club. The cards, issued to a number of subscribers, pay for their own printing but do not cover the cost of composition in the Bulletin nor the salary of the Bibliographer. It costs the Club more to print an issue of the *Index* than an average scientific paper. (2) Many workers in physiology and other experimental fields complain that an index of American work is of little use to them. Their interest in botanical publications has no regard to the nationality of the authors. Furthermore the titles that interest them are listed, classified according to subject, in Biological Abstracts, the Agricultural Index, or similar publications.

Since some modification of the *Index* may be desirable, it is hoped that you will give the questions below your prompt and careful attention, and return your answers and comments to the editor.

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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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A METHOD FOR DESCRIBING AND COMPARING
BLOOMING-SEASONS

EDGAR ANDERSON AND LESLIE HUBRICHT

(WITH SIX FIGURES)

For practical reasons connected with the management of the wild-flower reservation of the Missouri Botanical Garden's Arboretum at Gray Summit, Missouri, records of flowering-dates for about 100 species have been made there since September 1937. The species selected were those of particular interest to the public either because they made beautiful displays in the landscape (*Mertensia virginica, Coreopsis lanceolata*, etc.) or were particularly odd or interesting. (*Spiranthes gracilis, Arisaema Dracontium*, etc.) (Anderson 1937). These 100 species were scored once a week throughout the blooming-season (so far as possible) and were recorded as: 'coming into flower,' 'in full bloom,' 'passing out of flower,' or 'out of bloom.' In those borderline cases when it was difficult to say whether a species should be recorded in one category or another, the decision was made with reference to its landscape effect. *Viola striata*, for instance, has the habit of producing a very few flowers long after the main blooming-period is over. It was scored as 'passing out of bloom' as long as it gave that general effect. When the flowers became so few that they could not be found without getting down and searching among the leaves, the species was scored as 'out of bloom.'

As the data began to accumulate it became apparent that they could be put to various uses in addition to the utilitarian ones for which they had been gathered. In particular it occurred to us that by assigning numerical values to the scores it would be possible to add up the totals for each week and in this way produce a picture of the rise and fall of bloom throughout the season.

Such a curve could be used to compare different blooming-seasons or to compare the season of bloom in one locality with that in another. Quantitative values were therefore assigned to the records: 'full bloom,' three; 'coming into bloom,' one; and 'going out of bloom,' two, these values being approximately proportional to the landscape effect of the three conditions.

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The curve derived from these weekly totals is shown in figure 1, which gives a complete record for 1938 and such data as are available for 1937 and 1939.

As is shown in figure 1 the blooming-season at Gray Summit begins about the first of March and rises sharply for about eight weeks, then declines almost as rapidly for another eight weeks. After a two-week lull it increases slowly to another peak in midsummer. In favorable seasons the falling off from this peak is halted and the curve may even rise for a week or two when the autumnal Compositae come into bloom in September. There is in other words a sharp spring peak and a broader one in late summer separated by a distinct lull in late spring and early summer.
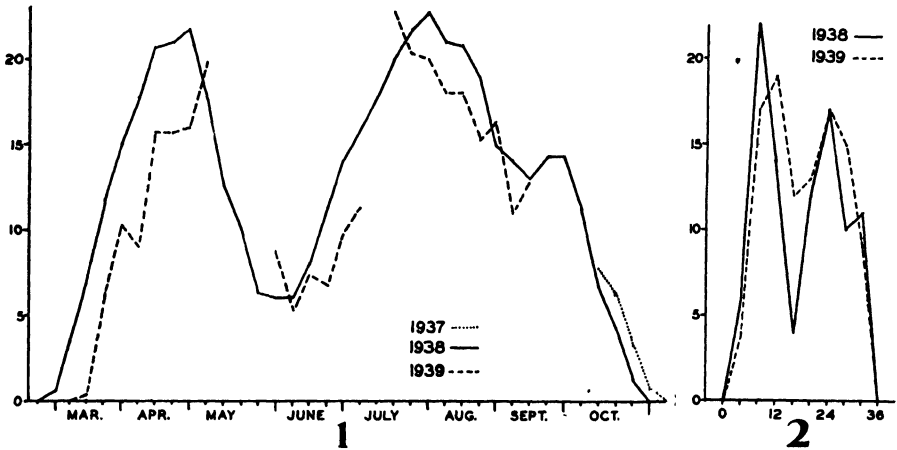
FIG. 1. Number of species in full bloom each week.
FIG. 2. Number of species at peak of bloom, by four week periods.

While the pronounced division into spring and summer bloom in Missouri has doubtless been noted by other observers, the only printed reference which has come to our notice is by Mrs. Rickett (1937, p. 69).

While the graph in figure 1 is based on roughly one-sixth of the species of native flowering plants, it is apparently a random selection, so far as blooming-dates are concerned. Certainly the large groups of plants that were not recorded present the same general features. The Amentiferae, for instance, would all coincide with the spring peak, the Cyperaceae and the Gramineae have high spring peaks and lower ones in late summer.

The curve shown in figure 1, while it presents an accurate picture of the wealth of bloom throughout the season, is undesirable for purposes of analysis. It is the resultant of two different effects; (1) the number of species coming into flower throughout the season and (2) the length of time these species remain in bloom. As can be seen from the original data in table 1, length of bloom not only varies from species to species but the average length of bloom in the summer is much longer than that in spring. By adapting a

suggestion of Prof. N. C. Fassett it was possible, however, to separate these two effects, and the curves shown in figures 2, 5, and 6 show the seasonal progression of number of species without reference to the length of time they remain in bloom. This was done by determining the middle of each species' blooming-period and graphing the number of these in every four-week period throughout the season.

The corrected curves for 1938 and 1939 are shown in figure 2 (the incomplete data for 1939 have been supplemented by estimates derived from the 1938 data and from observations made in previous years). It will be seen that the corrected curve presents the same general picture of spring and summer peaks of bloom separated by a less active period in early summer and that the curves for the two years are quite similar.
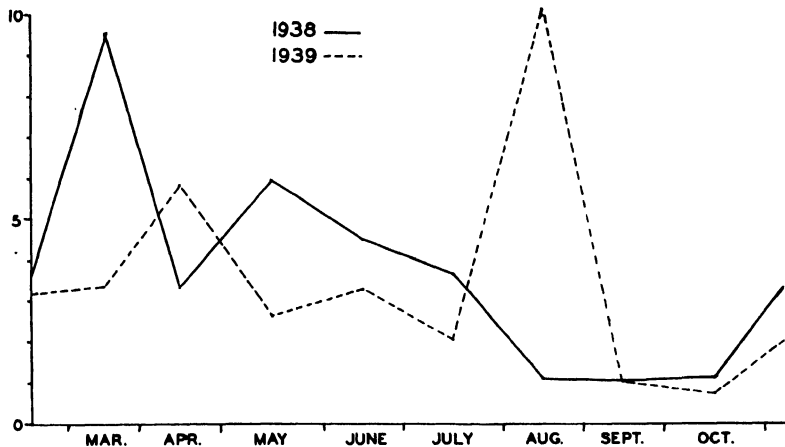
Fig. 3. Inches of rainfall at St. Louis, Mo., by months.

It is one thing to demonstrate such a curve but quite another to analyze the forces behind it. For the present we shall do no more than to outline some of the complexities involved in its correct interpretation. It is certainly affected by both environmental and inherent factors.

The effect of the environment is difficult to interpret because it is dual, the immediate effect, and its effect through natural selection. Both of these are particularly evident in the blooming-dates of those species which flower in the spring woodlands. The spring peak coincides with the time when the majority of trees are coming rapidly into full leaf and most of the bloom in the spring woods is over by the time the leaves are fully expanded. The spring flowers come on with a rush, as if in a hurry to blossom and go to seed while the woodlands are still sunny. However, they blossom in the same way and at the same time if transplanted to full sun. Evidently, therefore, these species have evolved in woodland habitats and have for generations

TABLE 1

Data on blooming-seasons of 96 species growing at Gray Summit, Mo., arranged according to the three major habitats; glades, woods, and meadows. Symbols under 'Origin' indicate probable center of distribution: C = Coastal Plain; I = Interior Plateaus; O = Ozark-Texas; and X = Uncertain. Each species was scored once each week: Blank = not in flower; 1 = coming into flower; 2 = passing out of flower; 3 = in full flower. Further explanation in the text.

	Origin	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
GLADES									
Allium stellatum	O						1 3 3	3 3 3	
Nothoscordum bivalve	C	1 3	3 3 2						2
Camassia scillioides	I		1 1 3 2						
Agave virginica	C					3 3 3 3	3		
Nemastylis acuta	O		1 3 3		1				
Spiranthes gracilis	I					1	3 3 3 2	1 3 3	
Spiranthes cernua	X								3 3 2 1
Arenaria patula	I		1 3	3 3					
Clematis Fremontii	O		1 3	3 3 2					
Delphinium carolinianum	X			1 3 3	3 2				
Leavenworthia uniflora	I		1 3 2						
Petalostemum purpureum	I				1 3	3 2			
Oenothera missourensis	O			1 3 3 2	2				
Asclepias tuberosa	C				1 3 3 2	2 1 3 3			
Asclepias verticillata	C				1 3	3 3			
Heliotropium tenellum	O				1 3 3	1 3 3 3	3 3 3		
Lithospermum canescens	O	1	3 3 3	1 3 3 2					
Scutellaria parvula	I			3 3 3	2				
Ruellia caroliniensis	C				1 3 3	3 3 3 3	3 3 3 2		
Houstonia angustifolia	O				1 3 3	3 3 3 3	3 3 3 2	2	
Vernonia crinita	O					1 1	3 3 3 3		
Liatris cylindracea	O					1 3 3	3 3 3 3	3 3 2	
Liatris pycnostachya	O					1 3 3	1 1 1	1 1 1 1	3 3 3 2
Aster oblongifolius	I								
Silphium laciniatum	O				1 3	1 1 3 3	3		
Rudbeckia missouriensis	O					1 1 3 3	3 3 2 1		
Echinacea pallida	O			1 3 3	3 3 2				
Coreopsis lanceolata	C			1 3 3 2	3 2				

TABLE 1.—(*Continued*)

WOODS	Origin	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Arisaema triphyllum	I	, 1	3 3 3	2 3					
Arisaema Dracontium	I		3 3 3	3 3					
Tradescantia virginiana	I		3 3 3	3 3					
Tradescantia canaliculata	C		1	1 3 3 2					
Uvularia grandiflora	I	1 3	1 3 2						
Erythronium albidum	C	3 2							
Hexalectris spicata	I					1 3 3	3 2		
Silene stellata	I				1	3 3			
Claytonia virginica	I	1 3 3	2 3 3	3 3					
Isopyrum biternatum	I	1 3	2 3 3	3					
Aquilegia canadensis	I		1 3 3	3 3					
Delphinium tricorne	I	1 3	1 1 3	3 3					
Sanguinaria canadensis	I	3 2							
Iodanthus pinnatifidus	I	1 3 3	2 1	1 3 3					
Dentaria laciniata	I	1 3	3 3	3					
Amelanchier canadensis	I	1 3	1 3	3					
Cercis canadensis	O	1 3	3 3 3	3 2 3					
Astragalus distortus	I		3 3 3 3 2 3 2	3 2 3					
Viola pedata	I	1	3 3 3	2 3					
Viola striata	I	1	3 3 3	2 3					
Viola papilionacea	I	1 3	2 1 3 2 3 3	2 3 2 2					
Cornus florida	I		2 1 3 3	2					
Dodecatheon Meadia	I	1	1 3 3	2 3 3		1 3 3	2		
Phlox divaricata	I	1	3 3	2 3					
Phlox paniculata	I					1 3 3			
Polemonium reptans	I	1	3 3	2 3 3					
Hydrophyllum appendiculatum	I		3 1 1	2 3 3					
Phacelia Purshii	I		1 1						
Mertensia virginica	I	1	3 2						
Monarda Bradburiana	O	1	1	3 3 3 2	1	3 3 3 2	3 3 2 3	3 3 3	
Veronicastrum virginicum	I					3 3 3 2		3 3 3	
Viburnum rufidulum	I		1 3	3					
Campanula americana	I					1 3 3	3 3 2 3	3 3 3	2
Lobelia siphilitica	I					1	1 1 3	3 3 3	3 2
Eupatorium urticaefolium	I					1 3	3 3 3	3 3 3	3 2

TABLE 1.—(Continued)

	Origin	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Woods (*Continued*)									
Eupatorium coelestinum	C							3 3	2
Solidago ulmifolia	I					1 3	1 1 3	3 2	2
Aster patens	I						3 3	1 3	2 2 2
Aster turbinellus	O						1	1 1 3	3 3 3
Aster anomalus	O							1 1 3	3 3 3
Aster Drummondii	O							1 3	2 3 3
Aster sagittifolius	I					1 1 3	3 3 3	1 3	3 3 3
Rudbeckia triloba	I					3 2 2	3 3 3	2 2	2 2
Rudbeckia laciniata	I					1	1	2 2	
Ratibida pinnata	I				1 3	3 2			
Meadows									
Iris virginica	C			1 3 3					
Rosa setigera	I			3 3 2	1 3 3				
Cassia fasciculata	C					1 3 3	3 3 3	2	
Hibiscus militaris	C					1 3	3 2 1		
Sabatia angularis	C			3 3 2		3 3 3	3 3	3	
Amsonia illustris	O		1	3 3 2					
Physostegia virginiana	I				1	3 3	1 3 3	3 3	
Monarda fistulosa	I			3 3 3	3 2	3 3	1 2		
Penstemon Digitalis	I		1	3 3 3	3 2	3 3 3	1 3 3	3 3	
Gerardia tenuifolia	I					3 3 3	3 3	3 2	
Campsis radicans	C				1 3	3 3 3	3 3	3 2	
Cephalanthus occidentalis	C					1 1 3			
Houstonia minima	O	1 3 3	3 2						
Vernonia altissima	I				1	3 3	3 3	1 3 3	3 3 3
Vernonia Baldwini	O					1 3	3 2	3 3 3	3 3 3
Solidago altissima	I						1 1 1	1 3 3	2 2 2
Solidago serotina	I						1 1 1	3 3 3	3 3 3
Aster pilosus	X							1 1 3	3 3 3
Aster vimineus	I							1	3 3 3
Silphium perfoliatum	O				1 3 3	3 2 2	3 3 3	3 3 3	3 3 3
Rudbeckia hirta	I				1 3 3	3 2 2	3 3 3	3 3 1	
Helianthus sp.	X					1 3	1 3	1 1 3	
Bidens polylepis	O					2	1 3	3 3	2

been selected towards a type which could finish its blooming season by this time.

This dual effect of the habitat on blooming season is shown in figures 5 and 6. In figure 5 the species used in drawing the curves of figure 2 are graphed according to the habitat in which they occur at Gray Summit and separate curves are drawn for each. For this purpose the habitats are grouped as woods, meadows, and glades. The last of these terms follows local usage in the Ozarks and indicates a peculiar and interesting habitat which has not yet received the scientific study it deserves. In Missouri a glade designates a rocky treeless area from a few square feet to several acres
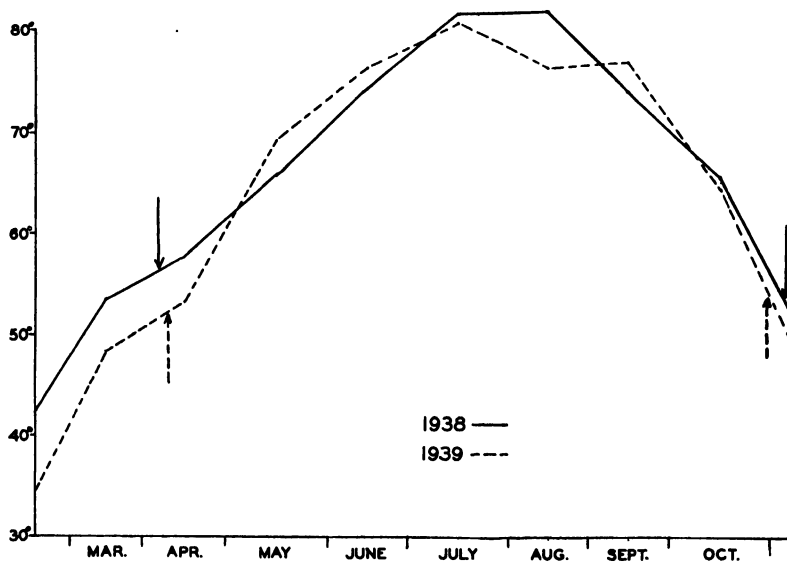
FIG. 4. Average monthly temperature at St. Louis, Mo. Arrows indicate last and first killing frosts.

in extent, somewhat analogous to the cedar barrens of Kentucky and Tennessee studied by Harper (1926) and Freeman (1933). The glades are even more closely allied to central parts of the Edwards Plateau and the Arbuckle Mountains. They are cold in winter, wet with seepage water in late winter and spring, and hot and dry throughout the summer.

It will be seen from figure 5 that the seasonal rhythm of bloom is radically different in the three habitats. The woodlands have the bulk of bloom in the spring, approach zero in early June and develop a lesser season of bloom in the late summer and fall. The treeless habitats are under no such pressure to blossom in early spring. Meadow-bloom rises rather slowly and more or less continuously to its peak in mid-summer. The glades are later to respond than either of these habitats and then maintain a fairly even amount of bloom throughout the year. Both the meadows and the glades,

however, show a drop in early June, though it is not so marked as that shown by the woodlands.

In figure 6 the species have been grouped according to the general character of their distributions. For this purpose distribution maps were prepared for each species. Inspection of these showed at least three main types of distribution (1) species centered upon the Gulf Coastal Plain (2) species centered on the Ozark-Texas axis and (3) species centered upon the interior plateaus of the Ohio-Mississippi River Basin (Anderson and Hubricht, unpublished). Most of the distributions could easily be placed in one of these three general categories, though a few had to be more or less arbitrarily assigned. The category to which each species was assigned is indicated in table 1. Some of the species are so poorly understood, taxonomically, that their distributions reflect their heterogeneity, and they have been omitted in
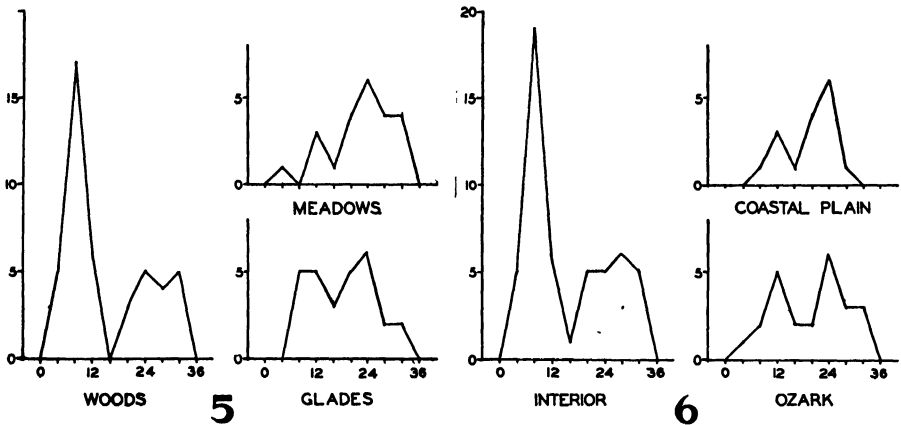
FIG. 5. Number of species at peak of bloom, grouped by habitats. Same scale as fig. 2.

FIG. 6. Number of species at peak of bloom, grouped according to probable center of distribution. Same scale as fig. 2.

preparing figure 6. It will be seen that the curves of figure 6 show the same general features as figure 5, though the two peaks of bloom are even more sharply revealed. A study of the data in table 1 will show that the groupings of figures 5 and 6 are very similar; most of the species of the central interior plateaus occur in the woodland, the glades are populated very largely by species from the Ozark-Texas axis, etc. Unfortunately the number of species for which we have information is too small to break up the curves still further in an attempt to distinguish between the direct and the selective effect of the habitats.

While the curves of figures 5 and 6 seem to give a rational though incomplete explanation of spring blooming-periods, they offer no clue as to why the summer peak should have the form that it does. The woods are

certainly as full of light in early June as in late July. Why then should we find *no* conspicuous woodland flowers in June but five or six species in July? Nor is there any evident correlation with either the temperature (fig. 4) or the rainfall (fig. 3). The most likely explanation would be that it is due to some kind of interaction with length of day. The last two decades have seen great progress in the interpretation of blooming-dates with regard to length of day (Garner 1937). It is now known that there are at least two funda-mentally different kinds of plants: 'short day' and 'long day.' Since the spring peak occurs during the period when days are lengthening, and the summer peak during that when they are shortening, it would seem that length of day is one of the factors involved. However, the maxima on the curve do not bear any simple relation to day length. The spring peak, for instance, does not in any way coincide with the greatest length (June 21) or with the greatest increase in length (March 21). If anything it comes closer to the latter than to the former and it may be that in a longer growing season the maxima would fall at the periods of maximum increase and decrease (March 21 and September 21). Obviously this is not a question which can be settled by records of blooming-dates from a single latitude. When similar statistics have been presented for other species and for other localities it may then be possible to discuss the phenomena authoritatively. It is with the hope that comparable records may be collected elsewhere on some of these same species that the original data for 1938 have been pre-sented in full in table 1. It would seem probable that if a group of these same species could be studied in the north they might show a single peak of bloom. Farther south one would expect an even wider division between peaks than is found in Missouri.

SUMMARY

1. A method is described for combining data on blooming-periods from various species to produce a generalized curve for an entire locality.

2. By the use of this method the blooming-season of 100 species native to Gray Summit, Missouri, was analyzed for 2 successive years. In their main features the 2 curves were similar. Each showed (a) a sharp peak of bloom in the spring (b) an almost equally abrupt cessation of bloom in early summer (c) a broad peak of bloom in late summer and autumn.

3. The interpretation of the factors responsible for these three features are discussed and the interplay of both environmental and inherent factors is suggested.

4. As a first step in analysis the above curve is broken down into separate curves for the three main types of habitat in the area and for the three chief distribution centers characterizing the species.

It is shown that the data from this one locality do not provide critical

evidence for evaluating the roles played by environment and germplasm in the determination of blooming-seasons.

5. The actual data are presented in tabulated form in the hope that comparable statistics may be collected for some of these same species at other localities.

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MICROSPOROGENESIS IN TRIPLOID AND DIPLOID PLANTS OF HEMEROCALLIS FULVA

CLYDE CHANDLER

INTRODUCTION

The object of this study is to compare the old and widely cultivated triploid clone, *Hemerocallis fulva* clone Europa, with wild diploid plants of this same species in respect to (1) the identity and structure of the chromosomes in each genom; (2) the behavior of these chromosomes in microsporogenesis; and (3) the extent and character of the various irregularities which result in the abortion of microspores.

Triploid clones in cultivation (Stout 1932) comprise: 1. the single-flowered (a) Europa Daylily and (b) the Maculata Daylily; 2. the double-flowered types known under the names of (a) Kwanso, (b) Flore Pleno, and (c) Variegated. All these plants are similar in habit of growth and color of flowers and all obviously belong to the somewhat variable wild species *H. fulva*.

The cytological studies already made of *H. fulva* may be grouped as follows:

1. Nearly all studies have been on *H. fulva* clone Europa. Many authors, e.g., Tangl (1882), Strasburger (1882), Biourge (1892), Juel (1897), Fullmer (1899), Schurhoff (1913), Tischler (1915), Belling (1925), Yamaha (1926), and Stout and Susa (1929), have studied plants of this clone and have been chiefly concerned with the numerous irregularities which occur during meiosis. Belling (1925) recognized that this clone is a triploid, and this condition affords a new interpretation of the earlier observations of much irregularity during meiosis.

Takenaka (1929) made studies of somatic cells in root tips of a plant which he called *H. fulva* and found the triploid number 33 chromosomes. His plant may or may not have been a member of the clone Europa.

2. A few studies have been made with other triploid clones of this species. Takenaka (1929) reported triploidy in a double-flowered clone which he called "*H. disticha* var. Kwanso." This is one of the old cultivated clones.

Another clone commonly designated as Flore Pleno was studied by Sienicka (1929). She reported irregular nuclear behavior during meiosis which results in polyspory. Unequal distribution of chromosomes at first division was recognized; however the chromosome number was not determined for this clone.

3. Some studies have been made of diploid plants. Takenaka (1929)

found the diploid number 22 in plants of "*H. disticha* Donn," and "*H. longituba*," both of which evidently are to be included in the species *H. fulva* (Stout 1934).

Dark (1932) studied a diploid plant of *H. fulva* which he considered to be of the type from which the triploid *H. fulva* clone Kwanso probably arose. Of the eleven chromosomes in a single genom, Dark distinguished three pairs of long chromosomes with median or sub-median attachment constrictions and from two to four pairs with sub-terminal attachments. In no other paper has an attempt to identify the chromosomes in any plant of *H. fulva* been reported.

4. Stout (1932) reported the result of cytological studies made on seedlings obtained by crossing the triploid fulvous daylilies, clone Europa and clone Maculata, with certain diploids. The majority of these seedlings were diploid, a few were triploid, and several were aneuploid with somatic numbers which fluctuated between the diploid and the triploid.

It is thus well established that the species *Hemerocallis fulva* comprises plants with a diploid number of 22 chromosomes and plants with a triploid number of 33 chromosomes.

The diploid number (22) has been well established in all the other species of *Hemerocallis* which have been investigated (Stout 1932, Takenaka 1929, Dark 1932, and Matsuura and Sutô 1935).

MATERIAL

The studies of the triploid condition to be reported in this paper are of the widely cultivated clone of the single-flowered fulvous daylily which was in cultivation in Europe as early as 1576 (Lobel 1576) and which has been propagated by vegetative means only. These plants are referred to as "*H. fulva* clone Europa" (Stout 1932). This clone is so completely self-incompatible that its members produce no seeds to self, close, or intra-clonal pollinations. Only a small percentage of the pollen formed is viable. The results of numerous hybridizing pollinations indicate that very few of the ovules are able to form seed in seed production. More than 5 seeds have never been obtained in any capsule (Stout and Chandler 1933). There are, then, two distinct types of sterility in the members of the clone Europa: (1) physiological incompatibilities in fertilization and (2) abortion of microspores, which is to be reported in detail in this paper.

In 1933 seeds of wild plants of *Hemerocallis fulva* were received from Albert N. Steward, who collected them near Lu Shan, Kiangsi Province, China. Plants grown from these seeds are now well established at the New York Botanical Garden, and it is from these diploid plants that material has been collected and studied for comparison with the triploid clone Europa.

METHODS

Aceto-carmine smears of pollen mother-cells were made according to Belling's method (1921), and made permanent by the method described by McClintock (1929). Some of these preparations have been kept in good condition for eight months by sealing them with a mixture of paraffin and gum mastic. The staining of the chromatin material in the early prophases was improved by adding a trace of Ehrlich's haematoxylin to the aceto-carmine, care being taken to prevent the formation of a precipitate.

Anthers from the young flower buds were fixed with Flemming's "medium" fluid, with Carnoy's, Nawashin's, Allen's modification of Bouin's, and chromo-acetic fixatives. Microtome sections were made from 7 to 24 µ in thickness. Flemming's triple stain, Heidenhain's haematoxylin, and Newton's gentian-violet-iodine combination were used. Feulgen's reaction was especially helpful in locating chromatin material often found in the cytoplasm outside the organized nucleus.

Smears (Warmke 1935, Heitz 1926) as well as paraffin sections of root tips were made. The fixatives and stains used for anthers were employed also for making permanent slides. Both cross and longitudinal sections were studied.

Mature pollen grains were prepared for study by the methyl green glycerine jelly method described by Wodehouse (1935).

Fig. 1. Semi-diagrammatic drawings showing the relative sizes and shapes of the eleven chromosomes of a genom of *Hemerocallis fulva* clone Europa.

THE IDENTITY AND NUMBER OF THE CHROMOSOMES

The three sets of eleven chromosomes each in the triploid *Hemerocallis fulva* clone Europa may be identified in somatic mitosis (fig. 1). In all cells the three homologous chromosomes are so alike that I have not been able to distinguish between them. These studies were made from prepared slides of root tips fixed with Flemming's medium fluid and stained with Heidenhain's haematoxylin and Flemming's triple combination. Each of the eleven chromosomes of a set has been identified.

The data presented in table 1 may be conveniently summarized as follows:

Four of the chromosomes, A, C, E, and K, have median attachment

TABLE 1

The chromosomes of the type clone of Hemerocallis Europa

Chromosome	Length in μ	Insertion region
A	4.25–4.25	Median
B	5.1	Sub-terminal
C	3.4 –3.4	Median
D	4.25–2.5	Sub-median
E	2.5 –2.5	Median
F	3.7	Terminal
G	5.9	Sub-terminal
H	5.1 –2.5	Sub-terminal
I	2.5	Terminal
J	5.9	Terminal
K	2.2	Median

regions, A being the largest and K the smallest. C and E can be identified only by careful measurements. Both D and H have sub-median insertion regions. The body of H is longer than that of D. Chromosomes B and G have sub-terminal attachment regions, G being the larger. F, I, and J appear to have terminal fiber attachment regions and can be distinguished by measurements.

In the diploid, the two sets of eleven chromosomes were identified; each chromosome is identical in appearance with a chromosome of the triploid.

MEIOSIS IN THE DIPLOID $(2n = 22)$ COMPARED WITH THAT OF THE TRIPLOID $(3n = 33)$

Prophases of the Heterotypic Division

In the early prophase stage in the diploid and triploid plants studied in this investigation, the nuclei are crowded with long fine zigzag chromatic threads which at a casual glance appear to form an irregular network. Closer study reveals that these threads are not continuous, but are a mass of single individual chromosomes. The pairing of homologous chromosomes in both diploid and triploid plants is always parasynaptic.

In the nucleus of the diploid at synapsis one large nucleolus is present. A definite nuclear membrane persists. Elongated chromatin threads, usually closely paired, chromomere for chromomere, throughout their entire length (fig. 2) are well distributed throughout the nuclear cavity. The chromomeres, first known as Pfitzner's granules (Pfitzner 1881) are of various sizes and appear spheroidal, but owing to their small size no further division of chromomeres into chromioles (Eisen 1899) has been observed. The chromomeres appear in a line surrounded by an achromatic matrix. Of the diploid it may be said that during the zygotene and pachytene stages there is close association of the homologs in each complement.

In the triploid the three homologs of the eleven chromosomal types have various degrees of association: (1) All three homologs may be rather closely
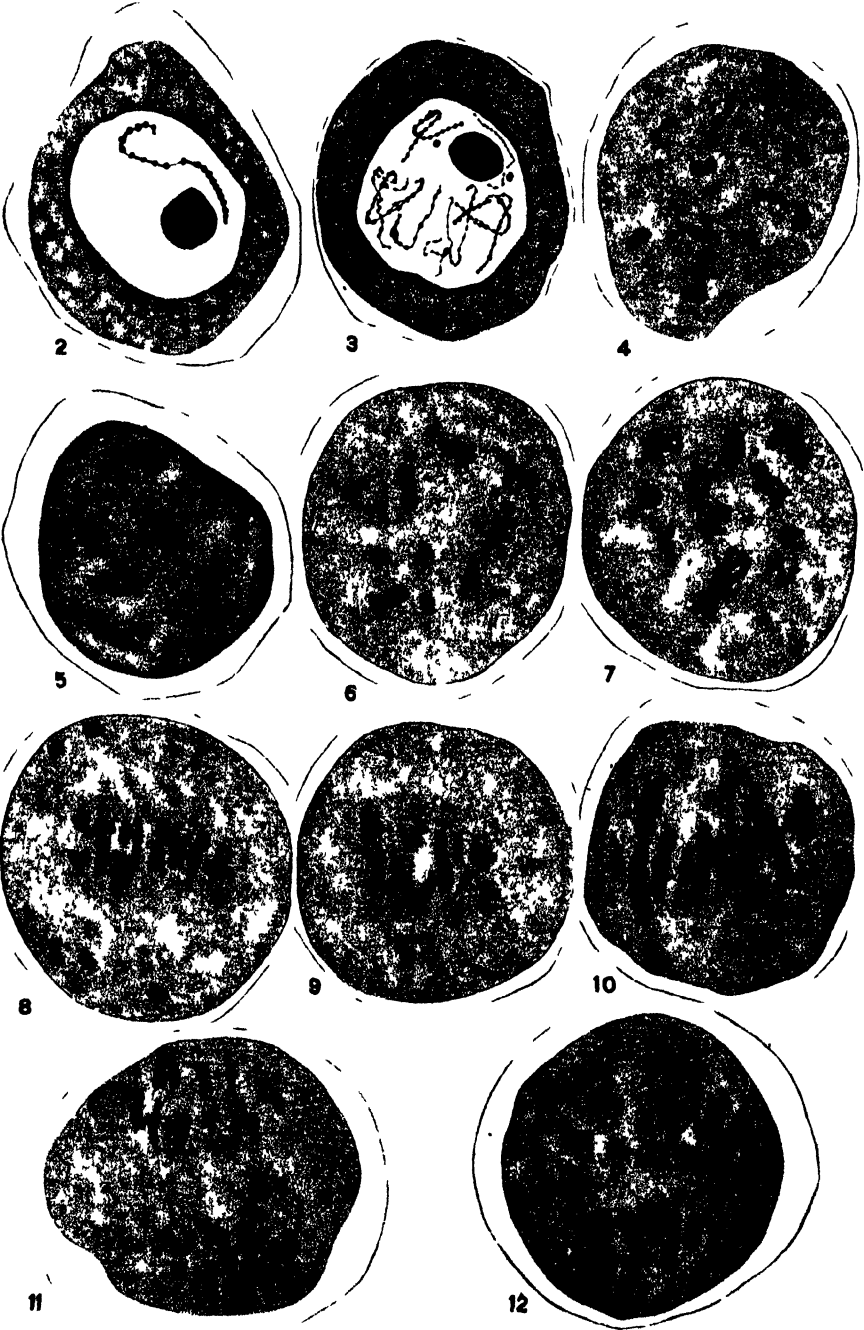
associated and very few of the chromomeres fail to become associated with other chromomeres. Though few workers have reported this type of association, it has been observed by Belling (1929) who was of the opinion that all three homologous chromosomes of a triploid hyacinth become completely synapsed, the threads forming a trihedral filament with flattened angles. Similar associations have been found in a few other species. Skovsted (1933) found in triploid Asiatic cotton some conjunct triple threads. Olmo (1934) did not observe triple synapsis throughout the length of the chromosome in the triploid *Nicotiana tabacum* but reports triple synapsis for a "considerable" length of the chromosome. He found that three general regions of the chromosome seem to favor triple synapsis: the large terminal chromomeres, the spindle fiber attachment regions, and lengths of the chromonemata in which prominent chromomeres are closely adjacent. It becomes evident that the degree of association of homologous chromosomes during early prophase depends upon the type of triploid studied. It is to be expected that the associations of homologous chromosomes of an autotriploid may be more complete than those of allotriploids or triploids having less homologous chromosomes.

(2) Close pairing of two of the homologs with very loose pairing of the third was seen. This type of association has been described for the majority of the triploids studied by previous investigators.

(3) A third chromosome may remain completely unassociated with the other two of its group. This behavior has been observed also in triploid

Explanation of Figures 2–12

FIG. 2.   Prophase of a pollen mother-cell of the diploid *H. fulva*, showing two homologous chromosomes synapsed at pachytene. Iron-haematoxylin. × 750.

FIG. 3.   Prophase of a pollen mother-cell of the triploid *H. fulva*, showing the associations of three homologous chromosomes at pachytene. Iron-haematoxylin. × 750.

FIG. 4.   Diakinesis in the diploid, showing eleven chromatin groups or eleven bivalents. Aceto-carmine. × 750.

FIG. 5.   Diakinesis in the triploid, showing thirteen chromatin groups which include 10 trivalents and three univalents. Aceto-carmine. × 750.

FIG. 6.   Late diakinesis in the diploid, showing eleven bivalents which are about to enter first metaphase. Aceto-carmine. × 750.

FIG. 7.   Late diakinesis in the triploid, showing eleven trivalents just before the first metaphase. Aceto-carmine. × 750.

FIG. 8.   Equatorial plate in the triploid, showing 5 univalents lagging at the periphery of the cell. Aceto-carmine. × 750.

FIG. 9.   Equatorial plate in the diploid. Homologs separating previous to first anaphase. Aceto-carmine. × 750.

FIG. 10. Equatorial plate in the triploid; the chromatin material is organized in irregular masses which may later form a pycnotic nucleus. Aceto-carmine. × 750.

FIG. 11. First anaphase in the diploid; the chromatids of the eleven chromosomes at each pole separating for the second division. Aceto-carmine. × 750.

FIG. 12. First anaphase in the triploid with 19 chromosomes at one pole and 14 at the the other. The distribution of chromosomes is as follows: A, A, B, B, C, C, D, D, E, E, F, G, G, H, I, I, J, J, and K. Total 19. A, B, C, D, E, F, F, G, H, H, I, J, K, and K. Total 14. Aceto-carmine. × 750.

Nicotiana tabacum by Olmo (1934) and in triploid wheat by Horton (1936). In prophase at zygotene and pachytene univalent, bivalent, and trivalent association of the three homologs of the eleven chromosome types can be seen (fig. 3). Horton has proposed the term "amphispireme" for this stage of meiosis in which paired and unpaired chromatin threads exist. Multivalents of more than three chromosomes which might be the result of structural hybridity, translocations, or inversions were not seen. At diakinesis two cells were seen in each of which were ten trivalents and three univalents. Further observations would possibly reveal this type of association in the earlier prophases.

Diakinesis

In the diploid there are eleven pairs of chromosomes. No unpaired chromatic elements were observed. The homologous chromosomes, each composed of two tightly coiled chromonemata, are much shortened at this time. The association is, however, rather loose. They are not, as in some plants, arranged peripherally within the nuclear membrane, but are scattered throughout the nuclear cavity (fig. 4). One spherical nucleolus is generally present in each nucleus. One and sometimes two chromosomes are often closely appressed against the surface of the nucleolus; but many nucleoli show no association with any chromosome. Two nucleoli are sometimes present in a single nucleus. During the later stages of diakinesis chiasmata were observed for the longer chromosomes (fig. 6).

In the triploid the three homologs of each of the eleven chromosome types may be associated in any one of the four ways previously described. A study was made (table 2) of the frequency and distribution of these associations among the eleven chromosomal types.

TABLE 2

Frequency and distribution of the associations among the eleven chromosome types during diakinesis

Number of cells	Number and type of configurations	Total number of chromosomes	Number of chromatin masses
18	11'''	33	11
41	10'''–1''–1'	33	12
2	10'''– 3'	33	13
35	9'''–2''–2'	33	13
1	9'''–1''–4'	33	14
22	8'''–3''–3'	33	14
5	7'''–4''–4'	33	15
2	6'''–5''–5'	33	16

It is clearly evident that in 18 of the nuclei there were complete associations of all three homologs of each chromosome type (figs. 5, 7). In the other 118 cells the associations were less complete and resulted in the forma-

tion of univalents, bivalents, and trivalents. In three cells in which all chromosomes were identified all three of the homologs of one of the chromosomal types remained completely unassociated.
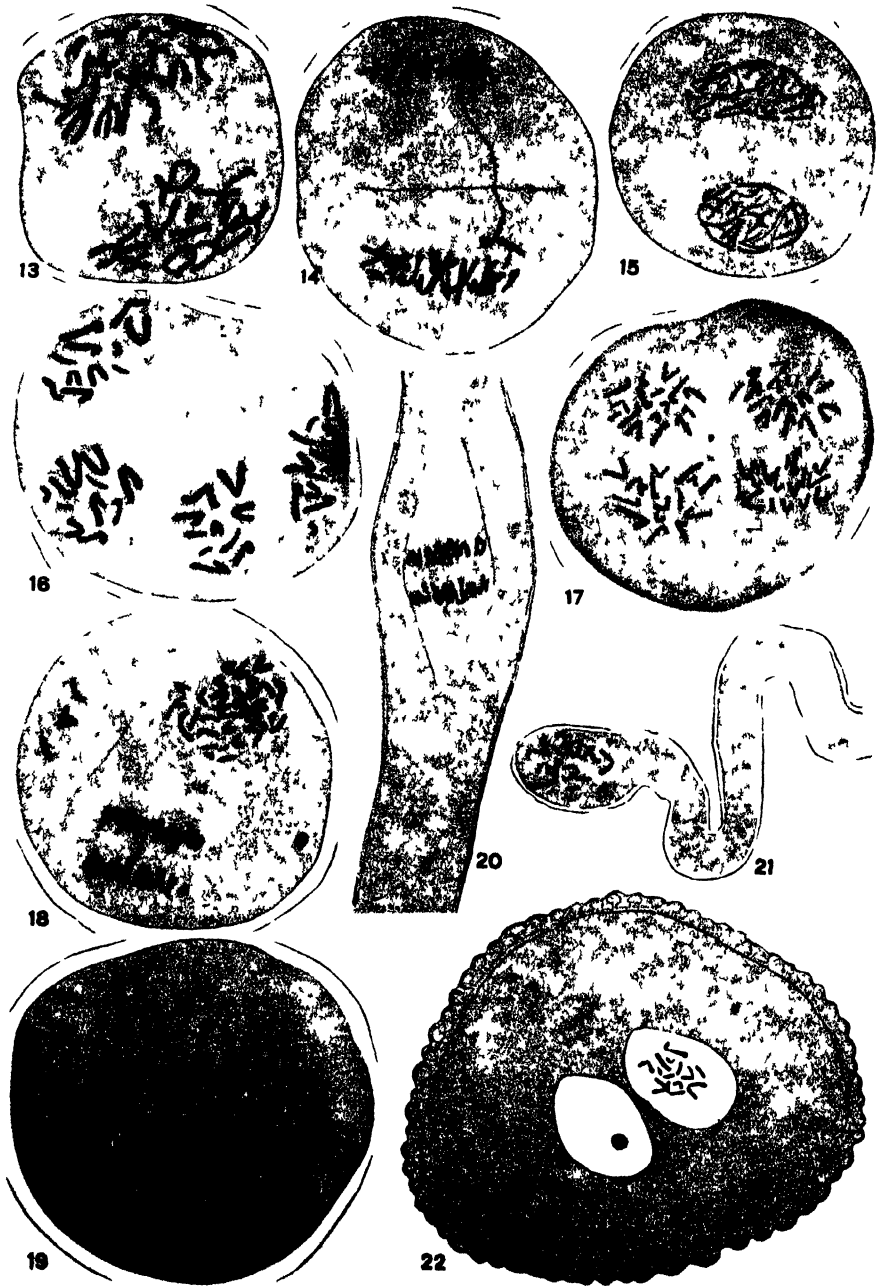
In each cell at diakinesis 33 chromosomes were present; none had disintegrated into the cytoplasm. Occasionally a pycnotic nucleus was seen in which the chromosomes had lost all identity and the chromatin material appeared in a knotted mass. This is evidently the beginning of disintegration of the chromatin material in the earlier stages of meiosis. In no pollen mother-cell was chromatin observed which had been discharged into the cytoplasm before first division in the manner reported by Timm (1928).

Metaphase of the First Division

In the diploid eleven bivalents are arranged in the equatorial region (fig. 9). At this time the homologs are closely associated and no unpaired chromatin elements are to be found. The chromosomes are short and thick. Chiasmata are in evidence. The chromatids are so tightly coiled that no further division or duplication is here visible, although such division or duplication probably occurs.

In the triploid eleven trivalents have occasionally been seen in the equatorial region. Varying numbers of trivalents, bivalents, and univalents are more frequent. This agrees with the reports of Belling (1925) and Takenaka (1929). It is often difficult to interpret the associations of chromosomes at metaphase, as may be seen in figure 10.

Explanation of Figures 13–22

FIG. 13. First anaphase in the diploid, showing elongated chromatids completely separated except at the insertion region. Aceto-carmine. × 750.

FIG. 14. First anaphase in the triploid, showing chromatids stretched across the equatorial region between the two poles. Aceto-carmine. × 750.

FIG. 15. Early telophase in the triploid. Aceto-carmine. × 750.

FIG. 16. Second anaphase in the diploid with eleven chromosomes at each pole.

FIG. 17. Second anaphase in the triploid with 16 chromosomes at two poles and 17 at the the other two poles.

FIG. 18. Second anaphase in the triploid, showing three lagging chromosomes and a microcyst formed at first division. Fourteen chromosomes in one cell and 17 in the other have duplicated and separated.

FIG. 19. In the triploid at the end of second anaphase cells were seen in which the chromatids have not undergone second division but remained associated at their insertion regions giving the characteristic X-shaped structures. Lagging chromosomes may under division and often have accessory spindles of their own.

FIG. 20. The generative nucleus in the diploid divides after it passes into the pollen tube. Eleven chromosomes passing to each pole. Carnoy's, gentian violet. × 750.

FIG. 21. The generative nucleus in the triploid may divide in the tube. Thirteen chromosomes may be identified. Three A chromosomes and one each of the other types are present here. Carnoy's, gentian violet. × 750.

FIG. 22. The generative nucleus in the triploid may divide within the microspore. Twelve chromosomes may be identified. Two K chromosomes and one each of the other types are present here. Carnoy's, gentian violet. × 750.

As many as five univalents have been seen lagging in the cytoplasm (fig. 8). These probably never reach the equatorial plate. Irregular distribution of chromosomes to the poles may be due in part to this failure of univalents to become oriented on the spindle. This will be more fully discussed later.

Anaphase of the First Division

In the diploid the homologous chromosomes associated at metaphase separate and move toward the respective poles. At this time the chromatids of each chromosome begin to separate, except at the insertion region, for the second meiotic division. In figure 11 it may be clearly seen that one homolog of each pair of chromosomes passes to each pole, and when they are somewhat scattered all may be identified at each pole. No unequal distribution or lagging of chromosomes has been observed at the first division in the diploid. The chromatids appear elongated and the sister chromatids are widely separated except at the insertion regions (fig. 13).

In the triploid clone both unequal distribution and lagging of chromosomes are prevalent (fig. 12). All chromosomes were identified in ten cells at first anaphase (table 3). For these observations cells showing the least irregularity in chromosomal distributions were selected. As in the earlier

TABLE 3

Distribution of identified chromosomes at first division

Cells	Pole I												Pole II											
	A	B	C	D	E	F	G	H	I	J	K	Total	A	B	C	D	E	F	G	H	I	J	K	Total
1	2	1	2	2	2	2	2	1	2	1	1	18	1	2	1	1	1	1	1	2	1	2	2	15
2	2	1	2	2	1	1	2	1	1	2	1	16	1	2	1	1	1	2	1	2	1	1	1	14
3	3	2	1	1	2			2	2	1	3	17*		1	2	2	1	3	3	1	1	2		16
4	1	2	2	2	2	2	2	1	1	1	1	17	2	1	1	1	1	1	1	2	2	2	2	16
5	3	2	1	2	2	2	2	1		2	2	19		1	2	1	1	1	1	2	1	1	1	12
6	2		2	2	3	2	1		1	3		16	1	3	1	1		1	2	3	2		3	17
7	1	2	1	2	3			2	1	1	1	14	2	1	2	1		3	1	2	2	3	2	19
8	2	1	3			3		1	2	1		13	1	2			3	2	1	2	3	3	3	20
9	1	2	1	1	2	1	1	2	1	1	1	14	2	1	2	2	1	2	2	1	2	2	2	19
10	2	2	2	2	2	1	2	1	2	2	1	19	1	1	1	1	1	2	1	2	1	1	2	14

Cells	Lagging Chromosomes												Grand Total
	A	B	C	D	E	F	G	H	I	J	K	Total	
1													33
2			1					1		1		3	33
3													33
4													33
5								2				2	33
6													33
7													33
8													33
9													33
10													33

* Chromatid stretched across equatorial plate from one pole to the other pole.

stages the three types of association between homologous chromosomes may be seen at this time. In nineteen cells the three homologs passed to the same pole. In two of these chromosome A behaved in this way; in one, chromosome B; in one, C; in one, D; in three, E; in two, F; in one, G; in one, H; in one, I; in three, J; and in three, K.

The distribution of chromosomes in other cells in which the chromosomes could be counted but not identified is shown in table 4.

TABLE 4

Distribution of unidentified chromosomes at first division

Pole I	Lags	Pole II	Total number of chromosomes	Number of cells
20		13	33	2
20	1	12	33	1
19		14	33	8
19	1	13	33	2
18		15	33	9
17		16	33	6
17	1	15	33	2
17	3	13	33	1
17	9	7	33	1
16	1	16	33	3

The study of 35 cells at the time when the chromosomes are passing to their respective poles during first anaphase shows that in most cells the chromosomes are rather evenly distributed to the two poles, the most frequent distributions being 18—15, 17—16, and 19—14.

Much irregularity in the distribution of chromosomes to the poles results from lagging chromosomes in the equatorial region. As many as nine have been observed about the equatorial plate after the other 24 chromosomes have moved to the poles. It is clearly evident that these different irregularities which end in abortion of microspores are not to be attributed to the aberrant behavior of any one chromosome. Evidently a mechanism which ordinarily functions effectively for the distribution of chromosomes into two equal groups when only two genoms are involved does not operate to distribute the chromosomes into equal groups when three genoms are present. As few as seven chromosomes may be seen at one pole. Further irregularities, such as the formation of the chromatin bridges previously noted in *H. fulva* by Juel (1897), Sienicka (1929), and Stout and Susa (1929), are not infrequent. Chromatin material may be stretched between the two poles, as seen in figure 14. It may be concluded that the chromatin bridges at the first anaphase result from the incomplete separation of chromatids due to the failure of terminalization of chiasmata.

A further study of 47 cells of the triploid at first anaphase and telophase

was made to determine the number of lagging chromosomes at first division. The numbers were as follows:

Number of Lags:	0	1	2	3	4	5	6	7	8
Number of Cells:	18	13	8	2	3	1	1	0	1

Twenty-nine cells (61.7 per cent) had lagging chromosomes. Eighteen cells (38.2 per cent) seem to have passed through first division without any loss of chromosomes or fragments of chromosomes. In the 13 cells in which a single chromosome was found lagging, various chromosomes have been identified. It is clearly evident that lagging is not a function of a particular chromosome.

The many irregularities in this triploid clone (*H. fulva* clone Europa) attracted the attention of earlier workers, such as Strasburger (1882). Takenaka (1929) reported unequal distribution of chromosomes at first anaphase, which gave "various combinations, e.g., 15, 18; 14, 18, 1; 14, 17, 1, 1; 16, 16, 1; etc." for the clone Kwanso. No mention of the frequency of the appearance of these various combinations was made.

During first anaphase it may be said that in the diploid there is an equal distribution of the chromosomes to their respective poles. No lagging was observed.

In the triploid unequal distribution of chromosomes to the poles, lagging chromosomes in the equatorial region, and chromatin bridges are prevalent.

Telophase of the First Division

In the diploid shortly after the eleven pairs of homologous chromosomes reach their respective poles the coils of the chromonemata loosen and a nuclear membrane is formed around the chromosomes. A deeply staining partition is formed in the equatorial region of the spindle, but cytokinesis is not completed at this time (fig. 37).

In the triploid as many as seven daughter nuclei were observed, each connected with two others by spindle fibers as shown in figure 29. It is evident from studies made at second telophase that such a pollen mother-cell may not undergo further division. Similar figures have been seen in anthers in which most of the pollen mother-cells were in second telophase.

The chromosomes which lag may completely lose their characteristic form and appear as homogeneous material (microcysts) held in small vacuoles of the cytoplasm (figs. 33–37; compare *Lilium tigrinum* as reported by Chandler, Porterfield, and Stout 1937); or they may round up into small

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Explanation of Figures 23–26

FIG. 23.   Mature pollen grains of the diploid. Methyl green glycerine jelly. × 85.
FIG. 24.   Mature pollen grains of the triploid. Methyl green glycerine jelly. × 85.
FIG. 25.   Germinating pollen of the diploid. Aceto-carmine. × 35.
FIG. 26.   Germinating pollen of the triploid. Aceto-carmine. × 35.
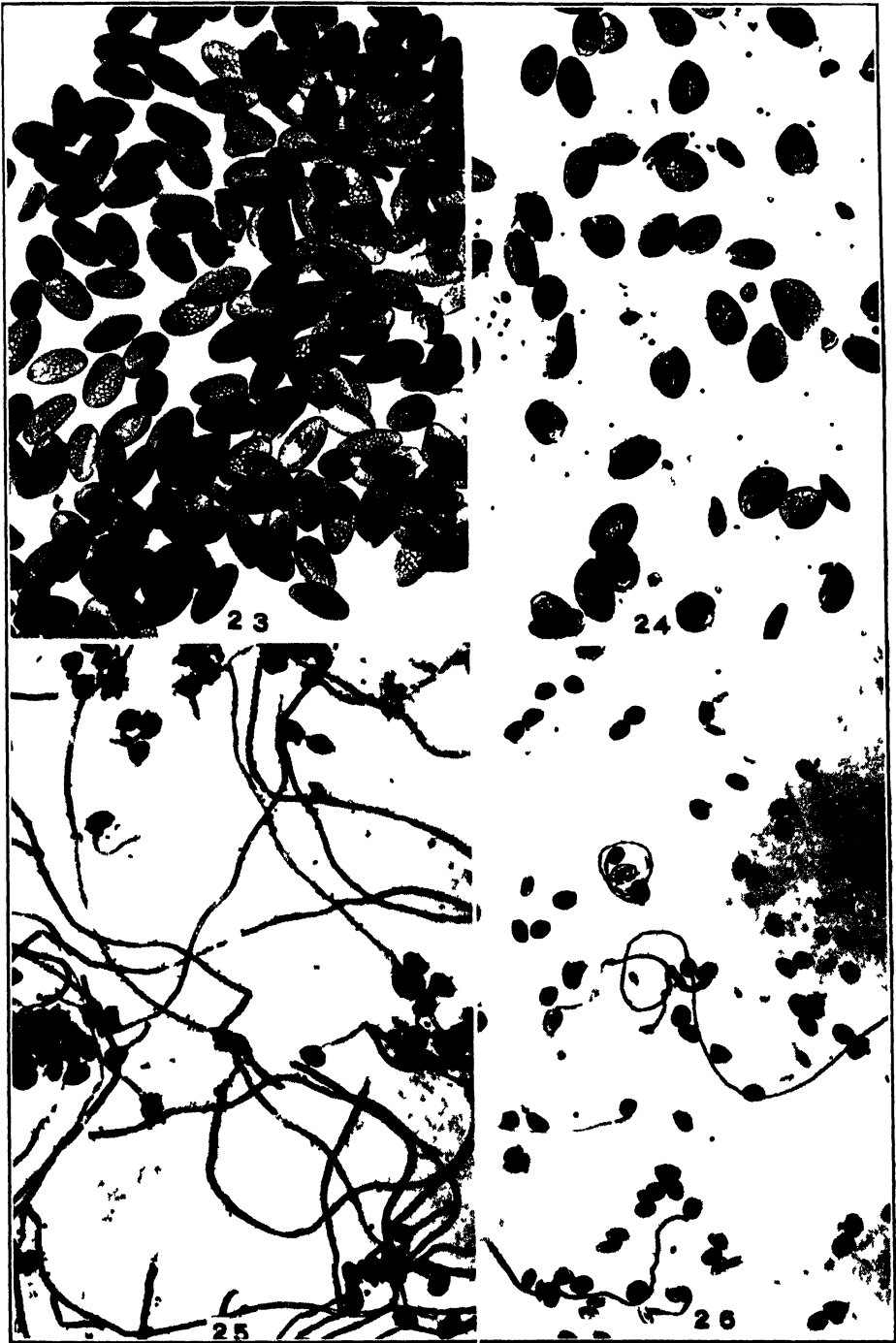
nuclei and be included in the cytoplasm as microcytes (fig. 32), in which case they may retain recognizable form (fig. 31). As many as four microcysts have been observed in the cytoplasm of a pollen mother-cell at the end of the first division (fig. 34). Lagging chromosomes may also be arranged on a spindle of their own and divide simultaneously with the other chromosomes of the cell (fig. 36).

Pollen mother-cells with pycnotic nuclei have been occasionally observed (fig. 27). The nucleus may not divide, in which case it usually becomes irregular in shape (fig. 28), or at the end of the first telophase the two nuclei may be undulated (fig. 30). The same figure shows that both microcysts and microcytes may be found in the same pollen mother-cell.
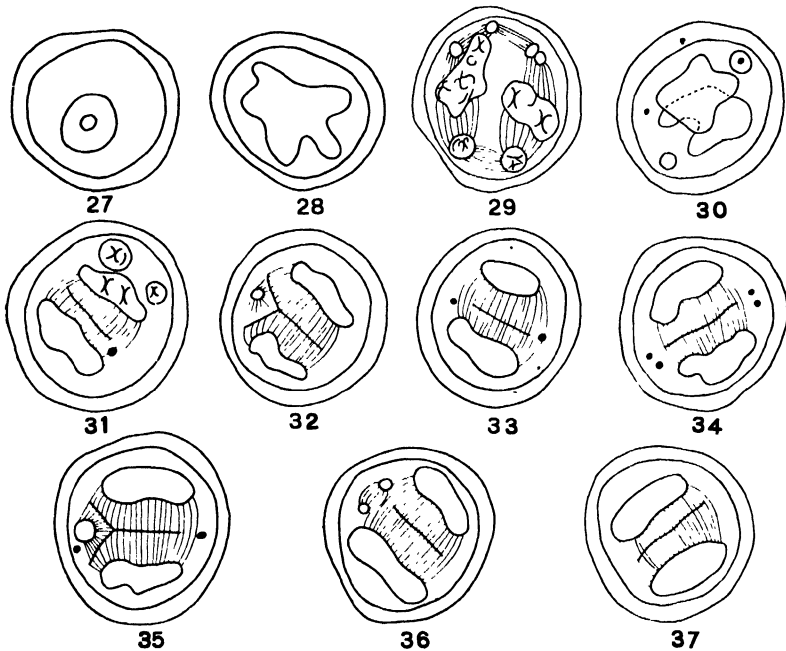
FIGS. 27–37. Camera lucida drawings of pollen mother-cells at the telophase of the first division in the triploid. FIG. 27. Pycnotic nucleus in pollen mother-cells in which there was no division of chromatin. FIG. 28. Undulated nucleus which has undergone no division. FIG. 29. Pollen mother-cell in which more than two nuclei were formed as a result of lagging chromosomes. These nuclei may or may not undergo further division. FIG. 30. Pollen mother-cell with two irregular nuclei, one microcyst, and two microcytes, one of which contains chromatin. FIG. 31. Nuclei and micronuclei in a pollen mother-cell in which the chromosomes are X-shaped owing to the separation of the chromatids for the second division. FIG. 32. Two nuclei and one micronucleus separated by a deeply staining partition. FIG. 33. Two microcysts formed from lagging chromosomes. FIG. 34. Two large nuclei and four microcysts within one pollen mother-cell wall. FIG. 35. Two microcysts and a microcyte formed during first telophase in addition to the two main nuclei. FIG. 36. Pollen mother-cell showing a small spindle formed in the division of lagging chromosomes. FIG. 37. Two nuclei formed by equal distribution of chromosomes, with no lagging chromosomes.

Fullmer (1899) states that bodies with the appearance of centrosomes are frequently seen at the poles. It seems quite possible that these microcytes and microcysts are the bodies to which Fullmer referred.

Interphase

During interphase in both diploid and triploid plants the two nuclei are fairly large and the two chromatids of each chromosome appear as somewhat slender, crooked, and apparently single threads joined or held together at the spindle attachment region only. The chromosomes are peripherally arranged (fig. 15) and are parallel and somewhat appressed to the newly formed nuclear membrane. They become much dispersed before the second division ensues. The chromatin material now stains more faintly than at any other stage during meiosis.

The Homoeotypic Division

In the prophase of the second division the condensing chromosomes, in both the diploid and the triploid, appear characteristically in the form of threads or rods still associated in dyads at their attachment regions but diverging elsewhere, somewhat less widely than during the previous anaphase. By the end of the second prophase matrices have became conspicuous about the chromonemata, and as the spindle develops the chromosomes become oriented in the equatorial region. At this time the chromosomes are considerably shorter and thicker than at the end of the first anaphase.

In both the diploid and the triploid it may be noted that during metaphase the chromosomes are now much shortened and thickened. The two sister chromatids assume a more parallel position and soon separate completely.

In the triploid microcysts and microcytes formed from first division lags as described by Chandler, Porterfield, and Stout (1937) are plainly visible at the periphery of the equatorial plate region.

In the diploid the second anaphase is regular and eleven chromosomes pass to each pole (fig. 16).

In the triploid the two sister nuclei often have the same number of chromosomes in the second division, but owing to lagging chromosomes at second anaphase this number may be unequal. Chromosomes which lag at this time may become vacuolated and dispersed in vacuoles of the cytoplasm and form microcysts, or they may form microcytes like those formed from lags at the first division. It has also been observed that the difference in the number of chromosomes in sister nuclei cannot be interpreted on the basis of lagging chromosomes alone. It is evident that sister chromosomes may be distributed to the same pole.

Chromatin bridges were also seen in cells at the second anaphase, though less frequently than during first anaphase. These are for the most part

formed between two chromatids of two homologs during the anaphase of the first division, which have persisted through the second anaphase. They may be recognized by their orientation toward the partitions formed at first and second divisions as well as toward the four chromosomal groups. Chromosomes which lag for a time in the equatorial region may later move toward the pole. One end of the chromosome may be held in the equatorial region, thus stretching chromatin material from the equator to one pole. This is a purely mechanical process which does not correspond in any way to the processes ordinarily involved in the formation of generally recognized chromatin bridges. The separation of sister chromosomes at the second anaphase may not proceed with exact precision, in which case the complete separation of two of the sister chromosomes may be delayed. In such cells during early anaphase chromatin material is stretched across the equatorial region. These may or may not persist (fig. 18).

It is difficult to obtain satisfactory preparations for the study of the distribution of chromosomes at the second division, since slight pressure on the cover glass does not scatter the chromosomes as it does in the anaphase of first division. The chromosomes in one figure will often spread so that identification of individual chromosomes is possible, but seldom can one identify all the chromosomes of all four groups. However, all 66 chromosomes were identified in five cells. In ten other cells it was possible to count and study the distribution of the chromosomes to their respective poles. As many as eight lags have been found in the spindle region at the homoeotypic division. In some cells no chromosomes were found lagging at second anaphase (fig. 17).

The studies of the distribution of chromosomes at the homoeotypic division in the triploid are summarized in table 5.

Thirty-one other cells at second anaphase and early telophase were studied with respect to the number of lagging chromosomes, with data as follows:

Number of lags:	0	1	2	3	4	5	6	7	8
Number of cells:	5	3	7	3	9	2	0	0	2

Lagging chromosomes as shown in figures 18 and 19 were observed in at least 80 per cent of the pollen mother-cells studied. In no cell was an entire set of eleven chromosomes observed among the laggards.

In the diploid during telophase of the homoeotypic division a partition is formed in the region of the equatorial plate perpendicular to the long axis of the spindle, which may be parallel or perpendicular to the partition formed at the end of the heterotypic division (fig. 38). The nucleus assumes the resting condition, which is typical for the nucleus of the pollen grain.

In the triploid the telophase proceeds in the same way when only four nuclei are formed. When lagging chromosomes are present, a small nucleus

TABLE 5

Distribution of chromosomes at second division

Cells	Pole I											Total	Pole II											Total
	A	B	C	D	E	F	G	H	I	J	K		A	B	C	D	E	F	G	H	I	J	K	
1	1	2	2	2	2	1	1	1	2	2	2	18	1	2	2	2	2	1	1	1	2	2	2	18
2	1	1	2	1	2	2	1	1	3	1	2	17	1	1	2	1	2	2	1	1	3	1	2	17
3	1	2	1	1	2	1	1	2	2	2		16	1	2	1	1	2	1	1	2	2	2		16
4	2	1	2	2	1	2	1	2	2	1	1	17	2	1	2	2	1	2	1	2	2	1	1	17
5	2	1	2	2		1	2	1	2		1	14	2	1	2	2	2		2	1	2	1	1	16
6												15												18
7												17												17
8												17												17
9												17												17
10												16												16
11												14												16
12												18												18
13												16												16
14												21												21
15												15												14

Cells	Pole III											Total	Pole IV											Total
	A	B	C	D	E	F	G	H	I	J	K		A	B	C	D	E	F	G	H	I	J	K	
1	2	1	1	1	1	2	2	2	1	1	1	15	2	1	1	1	1	2	2	2	1	1	1	15
2	2	2	1	2	1	1	1	1		1	1	13	2	2	1	2	1	1	3	3		1	1	17
3	2	1	2	2	1	2	2	2	1	1	1	17	2	1	2	2	1	2	2	2	1	1	1	17
4	1	2	1	1	2	1	2	1	1	2	2	16	1	2	1	1	2	1	2	1	1	2	2	16
5	1	1		1	2	2	1		1	1		10	1	3	2	1	2	2	1	1	1	2	2	17
6												16												17
7												16												16
8												15												16
9												15												16
10												17												17
11												17												15
12												15												15
13												17												17
14												12												12
15												15												16

Cells	Lagging Chromosomes											Total	Grand Total
	A	B	C	D	E	F	G	H	I	J	K		
1													66
2									2			2	66
3													66
4													66
5				1		3		2	2			8	66
6													66
7													66
8													66
9												1	66
10													66
11												4	66
12													66
13													66
14													66
15				1							1	2	66

may be organized about one or more of them and each lagging unit may retain its identity and become oriented in the cytoplasm, or it may lose its

identity, round up, and appear as a microcyst in the cytoplasm (fig. 30). By considering the position of the lagging units in the cytoplasm one can distinguish fairly accurately the laggards at first division from the laggards of second division (fig. 41). Chromosomes may remain in the cytoplasm without forming microcysts or microcytes and divide on small individual spindles at the end of second telophase (fig. 40). Microcytes may also be formed from chromosomes lagging at second division (fig. 39).
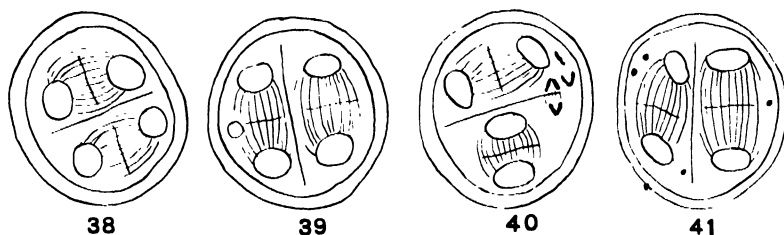
FIGS. 38–41. Pollen mother-cells at the telophase of the second division. FIG. 38. Four nuclei in a single pollen mother-cell. FIG. 39. Small nucleus formed from a second division lag, with the four nuclei usually formed. FIG. 40. A chromosome which lagged during first division and retained its individual form, dividing simultaneously with the other chromosomes in the cell. FIG. 41. Pollen mother-cell containing microcysts in the cytoplasm.

Division of the Cytosome

The writer has observed *in both the diploid and the triploid* that during late anaphase and telophase of the first division a dark staining partition is formed in the equatorial region of the spindle fibers and at right angles to the longest axis of the fibers. (See diagrams of first division in figs. 31–37.) Occasionally pollen mother-cells (figs. 27–30) were seen in which there was no division of the cytosome. At the telophase of second division a partition is formed in the equatorial region of each spindle perpendicular to the longest axis of the spindle as well as perpendicular to the partition formed at the end of first division (fig. 48).

Furrowing begins at the periphery of the cytoplasm and proceeds inward along the region of the partition formed during first telophase (fig. 44). Shortly thereafter (almost simultaneously) a furrow begins at the periphery of the cytoplasm and proceeds inward along the region of the partitions formed during second telophase (fig. 45). These furrows continue until the microspores are completely separated (figs. 46, 47). The mode of division of the cytosome is therefore a simultaneous one. Strasburger (1882) thought that in *Hemerocallis fulva* the cytosome divides as a result of successive cell plate formations, while Tangl reported that the pollen mother-cell divides into four cells simultaneously. Yamaha (1926) reported that this division in *H. fulva* may be either successive or simultaneous.

In the triploid a few pollen mother-cells have been observed in which no division of the chromatic or the cytoplasmic contents had occurred. A single

nucleus, irregular in outline, persists (fig. 42). The chromatin material appears clumped, and each clump seems homogenous throughout as though some process of disintegration of chromatin material were well under way.

Sometimes only two cells are formed from a pollen mother-cell as reported by Stout and Susa (1929). The chromosomes in these nuclei have their chromatids widely separated except at the insertion region, which gives them the characteristic appearance of an X, V, or W, depending upon the position of the insertion region. In these cells it seems evident that the homoeotypic division has not occurred (fig. 43). Small microcytes may occur in addition to the two large cells. In such cases more than two cells may be formed at the heterotypic division and these cells may not undergo any further division.

The lagging units of chromatin for the most part are oriented on small spindles which are quite distinct from the two larger spindles of the cell.
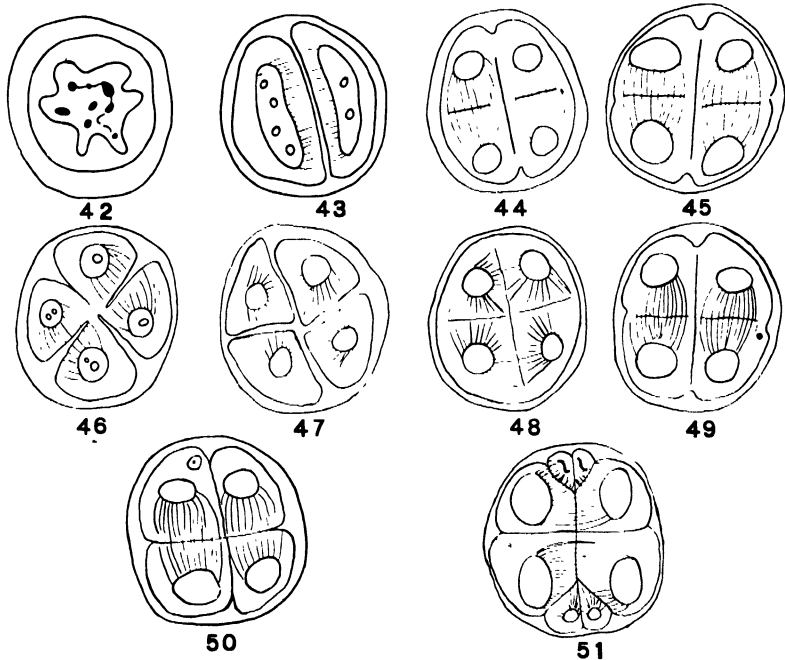
FIGS. 42–51. Division of the cytosome. FIG. 42. Amoeboid nucleus in which no division of chromatin occurred. FIG. 43. Two cells resulting from first division in which the homoeotypic division has not occurred. FIG. 44. Furrowing first begins in the plane of the partition formed at first division. FIG. 45. Furrowing proceeds simultaneously in the plane of the partition found at second division. FIG. 46. Furrowing proceeds from the periphery toward the center of the pollen mother-cell until the spores are completely separated as seen in fig. 47. FIG. 48. All four nuclei connected by spindle fibers. FIG. 49. Microcyst present in the cytoplasm at the end of second division. FIG. 50. Microcyte in the cytoplasm of the cell at the end of second division. FIG. 51. Through simultaneous furrowing microcytes are formed which result in very small microspores.

Partitions are formed in the equatorial region of the secondary spindles perpendicular to their longest axis. Through simultaneous furrowing small microspores are formed (fig. 51). Frequently microcytes or microcysts (figs. 49–50) remain in the cytoplasm of the microspore and have been observed in the mature pollen grains.

THE NUMBER OF MICROSPORES

For the diploid it is the rule that four microspores result from two regular divisions of a pollen mother-cell.

In triploid plants from one to twenty microspores have been seen within a single pollen mother-cell wall. The irregular number of microspores as well as their unequal size can be explained by the manner of chromosome distribution at both the first and the second divisions. The principal irregularities at this time are as follows (see table 6):

(1) Only two pollen mother cells have been seen in which there was no organization or division of chromatin (fig. 52).

(2) Two large cells within a single pollen mother-cell wall have been seen at the time when all surrounding pollen mother-cells have completed the homoeotypic division. Evidently only the heterotypic division occurred in these pollen mother-cells (fig. 53).

(3) Occasionally two large microspores with several smaller microspores have been observed within a single pollen mother-cell wall. From the appearance of the chromatin material in their nuclei, it is evident that they are the result of the heterotypic division and that no further division occurred. As many as ten microspores of various sizes may be formed at the end of first division.

(4) Frequently four large microspores with from one to four smaller microspores occur within a single pollen mother-cell wall (figs. 55, 56). It is clear from studies of second division metaphase that laggards of the first division may divide at second division. Four large spores may result from the two divisions of a pollen mother-cell (fig. 54).

(5) The smaller the microspores the fewer chromosomes there are in the nucleus of the spore. In cells where no cytoplasm is cut out and no nuclear membrane is formed about the lagging chromosomes, they round up, lose their characteristic shapes, and form· microcysts in the cytoplasm of the microspore (figs. 57, 61). A large number of microspores is due to the formation of more than two nuclei (as many as ten have been observed) with the division of many or all of these in the homoeotypic stage. As many as 20 small microspores were observed within a single pollen mother-cell wall (fig. 61). Occasionally four large and five or six small microspores (figs. 58, 59) or two large and eight smaller microspores were seen within a pollen mother-cell wall (fig. 60).
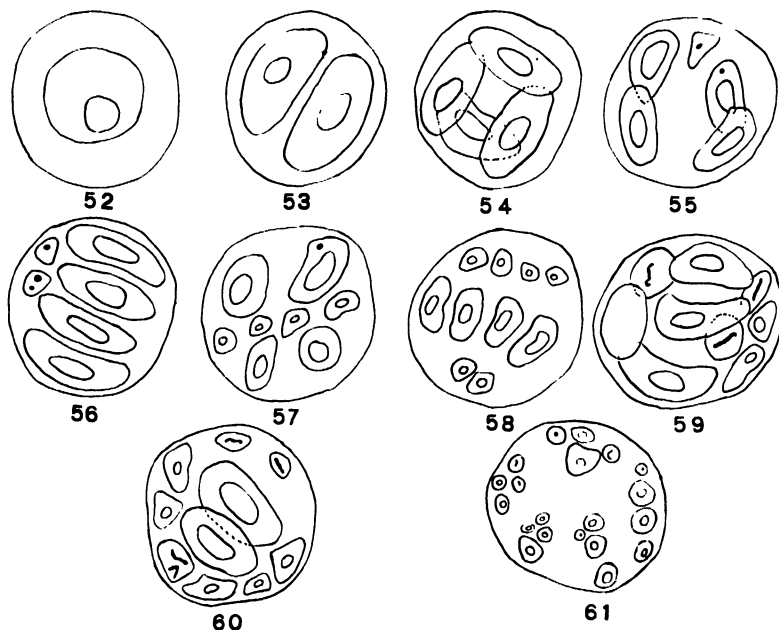
Figs. 52–61. Camera lucida outlines of ten pollen mother-cells containing different numbers of microspores. Fig. 52. Pollen mother-cell in which no division of nuclear material occurred. Fig. 53. Two cells which resulted from a single heterotypic division. Fig. 54. Four spores of nearly equal size. Fig. 55. Small cell containing microcyst but no nuclear organization, formed in addition to four cells of equal size, one of which contains a microcyst in its cytoplasm. Figs. 56–61. Increased numbers of cells from single pollen mother-cells; the majority have organized nuclei, others have microcysts in the cytoplasm or a single chromosome which has not been dispersed.

Four spores of approximately the same size were observed in only 26.6 per cent of the pollen mother-cells studied.

TABLE 6

Number and relative sizes of spores formed from single pollen mother-cells

Spores from one mother-cell			Frequency
1 large spore			2
2 large spores			2
2 " "	+2 small spores		1
2 " "	+8 " "		1
3 " "	+2 " "		4
3 " "	+4 " "		1
4 large spores			29
4 " "	+1 small spore		22
4 " "	+2 " spores		25
4 " "	+3 " "		8
4 " "	+4 " "		9
4 " "	+5 " "		1
4 " "	+6 " "		1
4 " "	+1 " "	+2 smaller	1
5 spores all about the same size			1
20 small spores			1

THE MICROSPORE NUCLEUS AND ITS DIVISION

From the present study of the microspore of the diploid it is clear that a single, large, spherical nucleus is present in each microspore. In only a few spores has this nucleus appeared to be irregular in shape.

In the triploid the microspores which appear most normal usually have one large spherical nucleus. In it thin chromatin threads form a fine network. However, in pollen grains of similar size the nucleus appears to be oblong, oval, crescent-shaped, or amoeboid in outline; such grains may not be viable. A single large nucleolus is usually present in each nucleus, although as many as five nucleoli have been seen in a single nucleus. A somewhat thickened wall is developed about each microspore. In case of further development the nucleus moves to the periphery of the cell, where mitosis and cell division produce a large vegetative cell and a smaller generative cell.'The latter soon migrates into the cytoplasm of the vegetative cell. This is completed at the time when the anthers are about four-fifths of their mature size.

The chromosomes in the early prophase of the mitosis of the microspore nucleus are long and comparatively straight. By the time they reach the equatorial plate they have become shortened to approximately one half the length seen in the earlier prophases. They are therefore compact and take stain very readily. In certain cells all chromosomes have been identified. The number of chromosomes participating in this division varies in different cells. The following numbers have been observed: 11 in one cell, 13 in one cell; 14 in four cells; 15 in two cells, 17 in two cells; and 18 in one cell. It is probable that further study would reveal a much lower number of chromosomes at the equatorial plate in mitosis of the vegetative nucleus, as reported by Stout and Susa (1929), who saw as few as six, or it might reveal as many as 22, which the breeding data suggest. It may be concluded that spores are formed which have other than eleven chromosomes.

MITOSIS OF THE GENERATIVE NUCLEUS

The generative cell divides to form two male gametes. This division may occur in the pollen grain before the pollen tube is formed or it may take place in the growing pollen tube.

The mitosis of the generative nucleus was studied in pollen tubes grown on artificial media. These preparations were prepared for study by the method described by Beatty (1937).

The pollen tube begins to protrude from the germinal aperture only a few minutes after pollen is scattered on the agar. Approximately two hours later the generative cell passes into the tube, and at the end of four hours early and late prophases, metaphases, and anaphases can be studied. In the diploid 11 chromosomes were frequently recognized at each pole of the anaphase (fig. 20).

In the triploid, mitosis of the generative nucleus was studied in the grain (fig. 22) as well as in the tube (fig. 21). In only a few tubes was the number of chromosomes determined for the generative nucleus. In one figure thirteen chromosomes were counted and identified. Presumably the variation in number would correspond to those in the vegetative cell.

VIABILITY OF THE POLLEN

It has been reported (Stout and Susa 1929) that germination of no more than 5 per cent was obtained for pollen of the triploid *H. fulva* clone Europa. Further tests of germination have given results in agreement with this earlier report. Only a few of the larger grains germinate (fig. 26). Many of the grains which do not germinate have protoplasmic contents. The pollen grains of the triploid are quite variable in size (fig. 24).

In the germination tests of pollen from the diploid at least 75 per cent of the grains produce long tubes (fig. 25). All the pollen grains have protoplasmic contents and appear to be quite uniform in size (fig. 23). Possibly the grains which did not germinate in these tests would do so with another treatment.

ABILITY OF POLLEN TO FUNCTION IN FERTILIZATION

There is much self- and cross-incompatibility in plants of *H. fulva*, but there has been no difficulty in obtaining seeds of diploid plants in pollinations that result in compatible fertilizations.

Twenty-three seedlings which have *H. fulva* clone Europa as one parent, either the seed parent or the pollen parent, and diploid daylilies for the other parent, have been grown at the New York Botanical Garden. The somatic numbers of chromosomes in these 23 plants ranged from 20 to 33. It seems evident (Stout 1932) that the gametes of the triploid which function most frequently in fertilization have 11 chromosomes, but that the number of chromosomes in functioning gametes may vary and rise to at least 22. The mechanism for the distribution of two sets of chromosomes into two equal groups or genoms does not seem adequate for the distribution of three sets into equal groups. Yet it does operate to the extent that some functional gametes are formed.

SUMMARY

1. The chromosomes have been identified in both diploid and triploid plants of *Hemerocallis fulva*. Two complete genoms of 11 chromosomes each were found in diploid plants grown from seed collected in China. Three such genoms were found in plants of the widely cultivated clone *H. fulva* clone Europa.

2. Meiosis proceeds regularly in the diploid plants and results in pollen grains of nearly uniform size, at least 75 per cent of which are viable when tested on artificial media.

3. The following irregularities have been found during meiosis in triploid plants:

a. The *associations* of homologous chromosomes in the early prophases are of four types. All three homologs may be rather closely associated and in such cases few chromomeres fail to become associated with other chromomeres. Close pairing of two of the homologs with a loose association of the third, which is the type described for the majority of triploids studied by various investigators, is frequent. A third chromosome may remain entirely unassociated. All three homologs of any one chromosome type may remain unassociated. These types of association result in the formation of univalents, bivalents, and trivalents.

b. The *distributions* of the chromosomes in the two divisions proceed with much irregularity and different numbers of chromosomes are distributed to the daughter nuclei. Lagging chromosomes were observed in the equatorial region at first and second anaphases. These later disintegrate in the cytoplasm, become vacuolated and dispersed in the vacuoles of the cytoplasm, thus forming microcysts, or become organized in small nuclei included in microcytes.

c. *Irregular numbers of nuclei* are formed at both the first and the second divisions as a result of the incomplete association of homologous chromosomes in the prophases, and of the unequal distribution of chromosomes during the first and second anaphases.

d. *Irregular numbers of microspores* are formed from a single pollen mother-cell. These vary in size, depending upon the number of chromosomes contained in their nuclei. In only 25 per cent of the pollen mother-cells studied were four spores formed that were nearly equal in size. As many as 20 small cells may be formed from one pollen mother-cell.

4. No more than five per cent of the mature pollen grains of this triploid clone germinate on artificial media. Owing to self-incompatibility no seeds have been obtained from this clone to self- or close-pollinations, but capsules are formed from certain hybridizing pollinations with other species and as many as five seeds have been obtained in one capsule. This low number of seeds in ovaries which contain as many as 30 ovules is evidence of abortion during megasporogenesis as during microsporogenesis.

5. The chromosomes of the diploid and of the triploid are remarkably alike in form, size, and shape. No evidence of structural hybridity was observed. It is evident that this triploid clone, Europa, arose from a diploid plant by autopolyploidy.

6. It is the general if not the universal rule that triploid plants exhibit much sterility due to abortion of spores. This is the condition even in autotriploids. In the Europa daylily, at least, the irregularities leading to abortions seem to be due to the third set of chromosomes and the effect which its members have on the mechanism of distribution.

The writer feels deeply indebted to Dr. A. B. Stout for his stimulating criticism and valuable suggestions during the progress of this study and in the preparation of this paper.

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INFECTION STUDIES ON THE COVERED SMUT OF OATS[1,2]

PAUL F. BRANDWEIN

Infection in the oat plant has been thought to be the result of a close relationship between the early development of the oat and the development of the smut, the environment playing a significant role. An investigation to determine the effective period of infection in the oat seedling seemed desirable and is here set forth.

This work is possible only through a technique by which 100 per cent infection of a susceptible variety was obtainable. Reed and Faris (25) present a method which involves dry spore inoculation of seeds whose hulls have been removed. These seeds are germinated under constant environmental conditions, optimum for infection. The discovery by Reed (19) that there are among the oat smuts certain physiologic races which differ in their ability to infect a selected oat variety made it possible to inoculate seed with smut of a known race.

REVIEW OF PREVIOUS WORK

In this paper it is not necessary to review the controversy whether the flower or the seedling is the original infection site. An excellent review of this question is offered by Kolk (14). It suffices to state that while several investigators[3] have offered evidence that flower infection occurs, it is equally evident from the work of others[4] that high infection percentages occur when the plant is infected by dry or germinated spores placed on the seed or seedling.

Some evidence is available to show that the young oat seedling may be infected, but not after the first leaf breaks through the coleoptile. Brefeld (5) described typical penetration holes in a three-day-old oat seedling and determined roughly the period of infection. He obtained 17–20 per cent infection of seedlings 2.5 mm. long, 7–10 per cent infection of seedlings 1 cm. long, and 2 per cent infection of seedlings 1.5–2 cm. long. Seedlings whose coleoptiles were penetrated by the first leaf yielded 0–1 per cent infection, whereas inoculation of older plant tissues and the growing point failed. He concluded, therefore, that the younger the seedling the more susceptible it is to infection.

Kolk (14) studied penetration and development of *Ustilago Avenae*. She states that the germ tubes from conidia may penetrate the oat coleoptile

at any place from its tip to its node. She did not find mycelium in the scutellum, the root node, or the lower portion of the mesocotyl of 1–4-day-old seedlings. In seedlings 5–8 days old the mycelium was distributed in the tissues of the coleoptile and mesocotyl. Kolk also found mycelium in the coleoptile of Black Mesdag, a variety resistant to the smut she was studying. Since then, Western (32) and Brandwein (3) have found considerable evidence from a number of oat varieties that the smut fungus may penetrate the coleoptile of resistant seedlings. Roesch (27) inoculated seedlings varying from 3 mm. to 3 cm. in length. He states that the infection period of the young oat seedling disappears with the eruption of the first leaf.

Studies on the physiology and ecology of infection augment the evidence obtained through histological investigation. McAlpine (17) suggested that whatever hinders the rapid development of the seedling and extends the periods of infection favors the access of the fungus to the growing point. Hiltner (10), however, maintains that while the highly susceptible Fichtelgebirg's oats penetrate the soil as rapidly as the resistant Ligowa variety, the former is markedly retarded in later development. This, according to Hiltner, may explain the greater susceptibility of Fichtelgebirg's oats. Reed and Faris (25) conclude that under controlled conditions of moisture, temperature, and soil reaction, the greater susceptibility to *Ustilago levis* of *Avena nuda* as compared with the Victor oat cannot be explained by differences in the rate of germination of the seeds. These authors, like McAlpine, raise the question of the apparent failure of very susceptible plants to give infection percentages of 100 per cent. They suggest that the explanation may be in the difference in the rate of growth of individual seedlings.

Since then Reed (24) has presented excellent evidence that infection of oats occurs in the seedling and that variation of nutrition and light in the post-seedling stage has no effect on infection. The evidence indicates that the first four days in the life of the plant are important and that treatment unfavorable to rapid growth of the plant in the post-seedling stage does not increase infection. Tapke (31), however, reports that environmental conditions after seedlings emerge may markedly influence the incidence of smut. He points out that the seedling-infecting smuts such as the loose smut of oats and the covered smut of barley invade their hosts during emergence of the seedling from the soil. Under "pre-emergence conditions" favorable for this smut invasion similar percentages of smut occurred in both the outdoor and greenhouse environments, while under "unfavorable·pre-emergence conditions" greenhouse plants had a higher incidence of smut than those grown in the field. Tapke concludes that "the rugged outdoor environment sustained and the temperate greenhouse conditions ameliorated the effects of the relatively unfavorable pre-emergence conditions." A proper evaluation of these results must await more complete data, since it must be based on a com-

plete knowledge of what is meant by "favorable" and "unfavorable" pre-emergence conditions."

On the basis of the data reported here, it seems safe to predict that an effective period of infection should be found in the oat seedling. The determination of such a period is itself of considerable interest and value in view of the various suggestions found in the literature. At the same time, some further knowledge may be gleaned about the structural or physiological modifications which the host undergoes as it passes from extreme susceptibility to a degree of immunity in the mature plant. It may be that this immunity of the mature susceptible plant is not physiological immunity of the growing point but is due to morphological changes involved in maturation.

Before proceeding further, it is necessary to establish a criterion of infection. In the normal relation between host and parasite, the smut fungus penetrates the oat seedling, establishes itself in the growing point, and forms chlamydospores at maturity. From the foregoing summary of the literature, it appears that the fungus may enter the oat seedling but may not sporulate. Yet it is clear that the latter condition is as much an infection as the former. For the purpose of description, infection of the oat may be defined as a relationship which terminates with the sporulation of the fungus. Any mention of infection in this paper should be interpreted in this way. However, opportunity will be taken in the discussion for a clarification of this question.

EXPERIMENTAL METHOD

Three varieties of *Avena sativa* L. were used in these experiments, Monarch (S.N. 161), Black Mesdag (S.N. 70), and Markton (S.N. 752). The smut used was *Ustilago levis* race 7, to which Monarch is 100 per cent susceptible, Black Mesdag partially susceptible, and Markton resistant. The smut, as well as the oat varieties, are propagated by Dr. G. M. Reed at the Brooklyn Botanic Garden.

The technique used in the inoculation, germination, and subsequent planting of the oats was the same as that previously described by the writer (3). For the purposes of this investigation, however, all seeds under 8 mm. in size were rejected. The seeds were germinated, groove downward, in sand contained in paraffined paper cups. The sand was moistened to 20 per cent of its water-holding capacity and the cups were placed in an incubator maintained at 20° C.

THE EFFECTIVE PERIOD OF INFECTION

To determine the effective period of infection, lots of seeds and seedlings were inoculated every six hours with dry chlamydospores. After the plants were generously dusted with spores from a rubber bulb, fresh sand of the same moisture content was carefully placed around and over them. Most of

the seedlings emerged from the sand 96–98[5] hours after planting; 12–16 hours later, rarely earlier, the first leaf broke through the coleoptile.

A summary of the results obtained is presented in table 1. The percentages of infection are the averages of the results of four plantings, two in the greenhouse in 1938 and 1939 and two in the field in 1937 and 1939.

TABLE 1

Infection of oat varieties inoculated with Ustilago levis race 7, at different hours

Hour inoculated	Probable period of infection	Monarch		Black Mesdag		Markton	
(from date of planting)	factor[1] 36–42 hours + inoculation time (column 1)	Number of plants	Percentage infection	Number of plants	Percentage infection	Number of plants	Percentage infection
0	36–42	110	100.0	110	79.0	110	2.7
6	42–48	110	99.1	110	85.5	108	0
12	48–54	108	100.0	106	61.3	105	0
18	54–60	106	100.0	107	46.7	102	1.9
24	60–66	110	100.0	105	40.9	110	0
30	66–72	106	98.1	104	46.6	109	0
36	72–78	104	91.4	100	37.0	108	0
42	78–84	106	84.9	109	27.5	107	0
48	84–90	105	86.7	106	32.1	110	0
54	90–96	110	63.6	99	19.1	97	0
60	96–102	104	56.7	103	8.7	104	0
66	102–108	101	69.3	108	0.0	102	0
72	108–114	106	33.0	100	1.0	89	0
78	114–120	100	28.0	100	3.0	101	0
84	120–126	98	10.2	91	0.0	88	0
90	126–132	97	5.2	102	0.0	101	0
96	132–138	102	4.9	106	0.0	100	0
102	138–144	94	2.1	90	2.2	99	0
108	144–150	104	0.0	103	0.0	107	0
114	150–156	105	0.0	102	0.0	105	0
120	156–162	108	0.0	98	0.0	110	0
126	162–168	106	1.9	110	0.0	110	0
132	168–174	105	0.0	102	0.0	108	0
138	174–180	107	0.0	103	0.0	109	0
144	180–186	108	0.0	101	0.0	107	0

[1] 36–42 hours is the approximate period of actual infection determined (table 2).

It was not thought desirable to carry out inoculation experiments with germinated spores, with conidia, or with smut mycelium, since the introduction of the inoculum would entail the addition of the medium in which it was grown.

Table 1 clearly demonstrates that the effective period of infection of susceptible and partially susceptible varieties occurs during the earliest stages of development. It further demonstrates that, as the seedlings develop, their

[5] The age of all the seedlings is calculated from the time at which the seeds were placed in sand.

capacity for infection is correspondingly limited. After the first leaf has emerged the capacity for infection is zero or nearly so.

A comparison of the three varieties is interesting. Markton, which is highly resistant, showed 2.7 per cent and 1.9 per cent infection respectively when inoculated at the zero and 18-hour stages, but was completely resistant thereafter. Black Mesdag, which is partly susceptible to *U. levis* race 7, gave infection percentages of 1, 3, and 2.2 after 66 hours, but 70.9 per cent and 85.5 per cent at zero and 6 hours, with figures decreasing to 8.7 per cent at 60 hours. On the other hand, Monarch showed 100 per cent infection (with some slight variations) through the 0–30-hour inoculation period, with percentages of infection decreasing to 4.9 per cent at 96 hours. After this period, subsequent inoculation produced 2.1 per cent infection at 102 hours and 1.9 per cent at 126 hours after planting.

Determination of the Actual Period of Infection

The data in table 1 become more significant when the actual time of infection is established. Since dusting of the seed with the chlamydospore is the method of inoculation used by many workers, this method was employed.

Preliminary experiments established that inoculation of seedlings exposed to air failed to cause infection. Since such exposure did not injure the seedlings it was possible to perform the following experiment. Seedlings 24 hours old were dusted with spores, covered with properly moistened inoculated sand, and placed at 20° C. At intervals of 20, 24, 28, 32, 36, 40, and 44 hours the cups were removed from the incubator, the surface sand removed, and the seedlings exposed to air. The cups were watered from below. Seedlings of Black Mesdag were similarly treated. The seedlings were transplanted to soil in pots from four to eight days after the emergence of the first leaf and grown to maturity.

Table 2 illustrates that for the Monarch oat, 40–44 hours contact with

TABLE 2

Infection time of oat seedlings inoculated with Ustilago levis race 7[1]

Time of exposure (elapsed hours)[2]	20	24	28	32	36	40	44
Percentage infection Black Mesdag	10.5	40	48.6	43.9	50	62.1	55
Percentage infection Monarch	15	27.2	59.8	90	91.4	100	100

[1] 40 seedlings were used in each determination, percentages being based on number of surviving plants.

[2] The 24 hour seedlings were all inoculated at the same time. "Time of exposure" indicates number of hours elapsed when the surface layer of sand was removed and the seedling exposed to air to stop infection; i.e., 24 hours added to "Time of Exposure" = age of seedling.

spores in sand resulted in 100 per cent infection. Twenty hours of exposure to the spores produced 10.5 per cent infection. This is in accordance with observations (Jones 16) that the dry spores may germinate within 6 to 24 hours under conditions suitable for germination. At the latter time, maximum germination appears to have occurred. Black Mesdag gave variable results; maximum infection appears to have occurred after 40 hours contact with spores in sand. Perhaps the infection percentage at 40 hours was maximum for that group of seedlings since, at best, infection percentages for Black Mesdag may vary from 50 to 85 per cent. It seems safe to consider from 36 to 42 hours as the period necessary for maximum infection of Monarch and Black Mesdag seedlings. It is conceivable, however, that seedlings in the later stages of maturity might require a longer period of contact with spores for infection to take place.

If table 1 is now examined more closely, it may be seen that infection of Monarch may be considered to occur during the period between 36 and 78 hours after planting in sand. This infection period is obtained by adding 36–42 hours to the inoculation period (column 2, table 1). During this 36–78-hour period, infection percentages of 100–91 per cent are obtained. After 78 hours from the time of planting, the infection percentages fall rapidly. Seedlings inoculated at 72 hours after planting were probably infected during a period of 20–40 hours (or slightly longer) after the inoculation (table 2), that is, at 92–112 hours after planting; while Monarch seedlings inoculated after 90 hours in sand were probably infected at 110–130 hours after planting. The latter period occurs after the emergence of the first leaf.

The figures for infection of Black Mesdag (table 1) are variable; the highest are those at the inoculation times of 0, 6, and 12 hours. At 30 hours after planting, there is a percentage of 46.6 infection, as compared with 61.3 per cent at 12 hours after planting.

The lower limit of the period of maximum infection for Black Mesdag occurs at about the same time as that for Monarch. Since Black Mesdag is only partially susceptible, a determination of a more exact limit of maximum infection time would have little value.

The seedlings most favorable for the study of penetration were 48–72 hours old, the evidence of penetration being very plentiful. Yet promycelia and conidia with fusion hyphae appeared to be as numerous during the 36-hour stage after planting as at the 72-hour stage.

It was necessary to ascertain whether seedlings could be infected during the first 36 hours. It had previously been found by Reed and Faris (25) that seedlings of Victor oats were not infected when they were germinated at 5° C. with 40 per cent moisture. It was thus possible to stop infection of Victor oats; possibly this could be applied to Monarch as well.

Two series of plantings were made. In one series, the seeds, planted in sand moistened to 20 per cent of its water holding capacity and maintained at 20° C., were inoculated with chlamydospores; in another, the seeds, planted in the same manner, were inoculated with spores germinated in a 2 per cent sucrose solution for 24 hours at room temperature. The latter bore abundant promycelia, conidia, and fusion hyphae. The solution containing germinating spores was applied with a pipette; accordingly the moisture content of these seedling cultures is somewhat higher. At six-hour intervals, the cups were removed from the incubator and the seedlings were transplanted in sand moistened to 40 per cent of its water-holding capacity and placed at 5° C. In one month most of the seedlings had penetrated the sand. In the inoculated control grown in sand at 40 per cent moisture and 5° C. one plant was infected out of a total of 36.

The results showed that up to 24 hours at 20° C. and 20 per cent moisture the infection by dry spores was zero, but with the germinated promycelia it was 8.4 per cent. After 42 hours maximum infection was reached, while after 36 hours 90.9 per cent infection was obtained with germinated spores. Nevertheless, we must question the accuracy of the results obtained with the germinated spores since numerous bacteria were found in all the cultures. On the other hand, plants inoculated with the dry chlamydospores were 72.5 per cent infected after 36 hours and 96.8 per cent infected after 42 hours at 20° C. and 20 per cent moisture. It seems that 100 per cent infection is uncertain before 42 hours when the seed is inoculated with the dry spores.

In the light of these experiments and suggestions in the literature, four stages may be suggested in the effective period of infection of the highly susceptible seedling Monarch. It must be emphasized that this refers only to conditions in which maximum infections of 100 per cent may be realized. These are as follows: (1) Lower limit of moderate infection; from 18 to approximately 36 hours after planting. (2) Period of maximum infection; from 36 to approximately 72 hours after planting. (3) Higher limit of moderate infection; from 72 hours to approximately 132 hours after planting. (4) Period of non-infection. This refers to stages past 132 hours in which inoculation of the normal plant with dry spores has been completely ineffective. A modification of this last point will be presented later.

A summary of the data from tables 1 and 2 shows that Black Mesdag, a form moderately susceptible to *Ustilago levis* race 7, has an effective period of infection limited to the first 100 hours, under the environmental conditions maintained. Of these 100 hours, the period between 36 and 54 hours after planting probably constitutes the effective period of maximum infection. On the other hand, Monarch, a completely susceptible variety, has an effective period of infection of approximately 132 hours. Of these 132 hours,

the period between 36 and 72 hours after planting probably constitutes the period of maximum infection. It is apparent that the susceptible variety has not only a longer effective period of infection but a longer effective period of maximum infection.

Correlation of Growth Rate and Maturation with Effective Period of Infection

Growth measurements of the three varieties, Monarch, Black Mesdag, and Markton, were made to determine whether their growth rate differed. All seedlings were grown under identical conditions at 20° C. in coarse sand of 20 per cent moisture content. Forty seedlings were removed from the sand every 12 hours over a four-day period and measured.

A comparison of the figures demonstrated that the growth rate of all was remarkably similar at every period. In fact all the seedlings germinated and penetrated the sand at approximately the same time. It is surprising that Monarch, the most susceptible of them all, grew slightly more rapidly than Black Mesdag or Markton. Obviously the greater susceptibility of Monarch cannot be explained on the basis of a difference in germination and growth rate. The foregoing experiments, however, throw some light on the nature of infection. It is seen that the highly susceptible Monarch, the moderately susceptible Black Mesdag, and the resistant Markton grow at approximately the same rate. It is equally clear that the effective period of infection for Black Mesdag is shorter than that of Monarch. It seems, then, that development in size masks a development of resistance to infection; the latter, however, is not correlated with development in size.

It is necessary to explain, however, why susceptible plants sometimes vary markedly in percentage of infection. McAlpine (17) tried to explain unequal infection on the assumption that the host plant must be at the right stage of development when the spore or conidium has put forth its germ tube and that this period does not last long.

In this paper evidence has been presented that a short period of infection does exist for the partly susceptible Black Mesdag. Furthermore, experience with growth measurements in seedlings of Black Mesdag shows the great variability in development at any one stage; this is also true of Monarch and Markton. Especially is this true of the difference in mesocotyl and coleoptile length of different seedlings. At 84 hours after planting, this variability is even more noticeable than it is at 72 hours. Beyer (2) also mentions the fact that this variability, especially of the mesocotyl length, has been a serious obstacle to all those who have attempted to study the physiology of the oat seedling.

THE REGION OF GREATEST INFECTION IN THE SEEDLING

McAlpine (17) remarks that unequal infection is the crux of the whole position; if we could account for it satisfactorily it would help us to under-

stand the conditions under which infection occurs. Two other types of experiments were planned, therefore, in the hope that the situation might be further clarified. One experiment was planned to determine the region of greatest infection in the seedling; another to determine whether or not it was possible to infect mature plants in the post-seedling stage, after the eruption of the first leaf. In this way it might be determined whether the immunity of the mature plant is due to a physiologic state or merely to the protection of the growing point by the outer tissues.

The method used to determine the regions of greatest infectibility was simple though tedious. For infection of the coleoptile tip the seedlings were surrounded by fine sand, with 1–2 mm. of the tips exposed to dusting with spores. For infection of the lower end of the shoot, about 2 mm. were exposed. Many methods were attempted; the most satisfactory was to place a hood of tinfoil over the seedling. Inoculations were made before planting and 48, 72, and 84 hours after. After inoculation, the hood was carefully removed and the seedling covered with coarse sand of the required moisture content. The seedlings were transplanted to pots in the greenhouse after the usual treatment.

The results are summarized in table 3. It is apparent that when different portions of the seed are inoculated, inoculation of the proximal end results

TABLE 3

Region of highest infection of Monarch oat seedlings[1]

Stage	Seed (at time of planting)		48 hours (after planting)		72 hours (after planting)		84 hours (after planting)	
Where inoculated	Proximal End	Distal End	Seed End	Coleoptile Tip	Seed End	Coleoptile Tip	Seed End	Coleoptile Tip
Percentage infection	100	15[2]	80[3]	20	24	24	0	2
Percentage infection Table 1 (Entire Plant)	100		85.7		33		10.2	

[1] About 2 mm. were exposed for inoculation; 50 seedlings were used for each regional inoculation.
[2] In these plants only the tillers were infected, not the main panicle.
[3] Five plants with tillers only infected.
[4] One plant with tillers only infected.

in the highest infection.   The 15 per cent infections obtained by inoculating the distal end may be due to faulty technique. It is possible that several spores or the developing mycelium reached the proximal end after the removal of the tinfoil. Theoretically, only one germinating chlamydospore is

necessary for infection. After 48 hours from planting, inoculation of the seed end of the seedling caused infection of 80 per cent, while 20 per cent were infected by inoculation of the tip. Infection of 2 per cent was obtained by inoculation of both seed end and coleoptile end of seedlings 72 hours old. No infection was obtained when the coleoptile tip or seed end of seedlings 84 hours old was inoculated. These seedlings were studied more carefully by inoculating successive areas beginning with the seed end of the shoot. They were treated as before, except that an additional 2–3 mm. were exposed at each inoculation. This 20 mm. shoot was thus divided into 7 regions. The results are summarized in table 4.

TABLE 4

Regional inoculation of the Monarch seedling[1]

Regions	Number infected	Number of plants	Region exposed
Seed end	0	10	Mesocotyl
6 mm.	0	10	Mesocotyl
9 mm.	0	9	Mesocotyl near coleoptile node
12 mm.	0	10	Lowest part of coleoptile below growing point and mesocotyl
15 mm.	1	9	Coleoptile node and mesocotyl
18 mm.	1	10	Coleoptile and mesocotyl
20 mm.	2[2]	10	Coleoptile and mesocotyl

[1] All seedlings were inoculated 84 hours after planting,
[2] 1 plant with tillers only infected.

It is apparent that inoculation of the mesocotyl caused no infection. Yet histological examination of the epidermis of such seedlings shows abundant penetration by the fungus of both mesocotyl and coleoptile. Kühn (15) working with bunt, maintained that infection was possible only through the portion of the seedling between the root node and coleoptile node. His conclusions, he thought, were strengthened by his discovery of germ tubes in the tissues of the coleoptile of barley seedlings which grew into sound plants. Lang (16), working with loose smut of oats, thought that the mesocotyl was the point of entry. Kolk (14) found mycelium in the coleoptile and the mesocotyl of 73 oat seedlings inoculated with loose smut. The results reported here indicate, however, that penetration and subsequent establishment of the fungus in the plant tissue does not mean infection in the sense that the parasite will sporulate.

A study of seedling growth shows that 48 hours after planting the seedling is about 4.5 mm. long. This is about 17 per cent of the entire growth (averaging 28 mm.) of four days. After 72 hours the seedling is about 14 mm. long; in the next twenty-four hours the seedling grows an additional 14 mm. In the last two days, 83 per cent of the entire four-day growth has

occurred, an increase in rate of approximately 480 per cent over that of the first two days.

The period of maximum infection has been shown to exist during the first 72 hours after germination. For Monarch, this period may be correlated with the early slow growth rate. Similarly the period of decreasing infection begins at 48 hours after planting; it is to be correlated with the very rapid growth rate after this time.

With the help of this evidence, the story of infection in completely susceptible varieties may be reconstructed as follows: When the seed is inoculated and placed under suitable environmental conditions, the spores germinate and the fungus penetrates the plant between 36 and 42 hours after planting. The fungus flourishes within the plant and eventually is established in the growing point, where it remains until sporulation. Spores, however, vary in their time of germination and the fungus may penetrate the base of the plant 72 hours after planting. If it does it may remain in the mesocotyl, which rapidly elongates, carrying with it the growing point. If the fungus penetrates earlier (60 hours after planting) it may eventually reach the root node, where it may remain until tillers are produced and infect the growing points of these. On the other hand, penetration by the fungus at the base of the plant 84–96 hours after planting will probably result in its establishment in the tissues beneath the growing point. Sporulation may not occur. If it is established in mesocotyl and coleoptile only, it will die when these structures degenerate.

While the mycelium may grow as rapidly in mature tissue as in the immature seedling, it is certain that a hypha entering at the seed end of a seedling 84 hours old must traverse over 11 mm. to reach the growing point.[6] If the fungus enters 24–36 hours after planting, it is directly on the level of the growing point. Examination of hyphae in the coleoptile and mesocotyl of Monarch seedlings show that they ramify in these tissues and do not grow straight towards the growing point. It is highly probable, therefore, that the hyphae may ramify in the coleoptile or mesocotyl and go no further, or they may reach the crown node or the growing point.

It is also probable that the growth of the mycelium in the mature plant is slower than that in the young seedling. Measurements of cells of oat seedlings 24, 48, 72, and 96 hours after planting show a great increase in length of these cells as the seedlings mature. About 20 cells in approximately similar localities were measured on strips of epidermis of five seedlings. The average length follows:

24 hours—30.2 μ	72 hours— 76.2 μ
48 hours—48.5 μ	96 hours—194.2 μ

[6] This figure is derived from a measurement of the average distance of the growing point from the seed end: about 11 mm. at 84 hours after planting.

The width of the cells increased proportionately. The cell walls increase in thickness from about 2μ (24 hours after planting) to about 4 or 5μ (60 hours after planting). Kolk (14) has shown that the hyphae she was studying tended to remain in the peripheral cytoplasm of the oat cell and did not penetrate the vacuole. There is sufficient reason to assume, therefore, that the smut mycelium may be retarded in its growth toward the growing point by the thicker walls, the larger cells, and by the tonoplast. Altogether, the distance the hypha must traverse, and the obstacles present in its path toward the growing point, help to account for the failure to realize always 100 per cent or other high infection percentages in seedlings of the Monarch oat inoculated 48 hours after planting.

While low percentages of infection of a highly susceptible variety may be satisfactorily explained on the basis of an increased growth rate and on maturation phenomena such as thickening of the cell wall, appearance of vacuoles, and cell elongation in the late seedling, this explanation may not be used for moderately susceptible and resistant varieties such as Black Mesdag and Markton. These two grow at a rate remarkably similar to that of Monarch. In other words, these two varieties should, if growth and maturation are the only factors to consider in immunity to smut infection, be infected as easily as Monarch.

INFECTION OF MATURE PLANTS THROUGH INOCULATION OF THE GROWING POINT

It was thought that inoculation of the growing point of mature plants should produce infection. Faris and Reed (8) have shown that mature injured plants of sorghum may be infected. Injections into the growing point and surrounding tissue of germinated and dry chlamydospores in various media by hypodermic needle failed to produce results in 1936, 1937, and 1938. Finally, in 1939, oat plants were successfully grown to maturity in paraffined paper cups and the following experiments proved successful. Plants were grown for three weeks during the spring growing period and for six weeks in the fall growing period. After this, the bottoms of the cups were pierced and the cups placed in moist chambers containing an inch of water. The leaves of the plants were removed and each plant was slit medially to the growing point node with a sharp razor. For three successive days, the plants were covered with a fine spray of a 1 per cent sucrose solution, then dusted with the dry chlamydospores. After one week and a half the covers were removed from the moist chambers. The plants were about 1.5 feet in height at fruiting.

The results, as may well be expected, were erratic. In one series of 30 Monarch plants, four were infected; in another series of 25 plants, 24 were infected. In Black Mesdag, 5 plants out of 52 were infected, while no infection of Markton could be obtained. An improved inoculation technique may

yield greater percentages of infection. On the basis of these results more significance may be attached to the role of rate of growth and maturation in decreasing the infection of a completely susceptible variety such as Monarch. The rapid rate of growth and maturation of the seedling presents certain obstacles to the smut fungus in its attempts to reach the growing point, which, however, remains susceptible.

With the discovery that oat seedlings could be grown to maturity in the paraffined paper cups, the three varieties were grown in this manner to determine whether post-seedling stunting of growth would increase infection. The percentages of infection of stunted plants were compared with those obtained by the writer for normal plants and found to be very similar.[7] At the same time, Dr. Reed (24) was conducting experiments which demonstrated that stunting the post-seedling plant by varying nutrition and light did not affect the percentage of infection. This is definite evidence that in oats the infection phenomena during approximately the first five days of the life of the plant are important. Modifications of growth or nutrition thereafter do not alter, at least in any externally visible characteristic, the relations between host and parasite established during these first few days.

Finally, it has been thought that a non-sporulating infection may adversely affect the oat varieties in which such infection is present. Brandwein (3), working with controlled conditions and known races of smut, could not substantiate the report of Hubbard and Stanton (11) that such varieties were adversely affected in yield and height through inoculation with smut. Stevens (30) also was unable to demonstrate an adverse effect on mature Markton plants. The work here presented further confirms the writer's previous work. Of the plants inoculated at different hours (table 1) many which had been inoculated 60–96 hours after planting produced normal main heads and were counted as non-infected. In no way could these plants be distinguished from others in the row or in the plot. Yet from one to two weeks later many of these plants produced infected tillers. Measurements of the height of main stalks, number of culms, and yield of these plants, and a comparison with an equal number of normal plants chosen at random from the same rows showed little difference, as can be seen from the following :

| | *Monarch* | | *Black Mesdag* | |
	Normal	*Infected Tillers*	*Normal*	*Infected Tillers*
Number of plants	31	31	23	23
Average height in cm.	71.2	73.9	80.7	78.7
Average number of culms	7.2	8.9	6.1	6.3
Weight of main head in gm.	2.3	2.2	2.9	3.0

[7] Monarch, normal plants, 100 per cent; stunted, 98 per cent infections. Markton, normal, 0; stunted, 0 infection. Black Mesdag, normal, 79 per cent; stunted, 68.8 per cent infections. There were approximately 100 plants in each series of normal and stunted plants.

This is to be expected if the fungus does not reach the growing point; it is in the panicle that it produces its characteristic spore masses. On the other hand, if the mycelium remains in the crown node, it may infect the growing points of the tillers.

Reed and Stanton (26), in a study of inheritance of resistance to the smut disease of Markton hybrids, found that in Markton and its hybrids with other varieties a few plants were observed which were described as "blasted." Such plants usually produced infertile spikelets. The spikelets of some plants were rudimentary, those of others were better developed but contained some smut spores. Through the kindness of Dr. Reed seeds of the various F_3 hybrids in which normal infection and blasting occurred were supplied to the writer. They were inoculated, planted, and grown in the greenhouse for three weeks in the fall of 1939. The growing points were then removed and examined histologically. Mycelium was detected in percentages which agreed closely with those given by Reed and Stanton for blasting in these Markton hybrids. It seems, therefore, that blasting may be due to smut infection. Perhaps the smut fungus reached the growing point in these hybrids, disorganized it, but could not complete its life cycle because of internal conditions unfavorable for its sustained growth. There is little cause to doubt that internal factors in Markton are unfavorable for the growth of the mycelium.

DISCUSSION

Much of the discussion of the data bearing on specific points has been presented under the various subdivisions of this paper. It is the purpose here to consider the data as it touches the general problem of systemic infection, with special reference to infection of the oat plant.

From reports in the literature and from this paper, it is apparent that all grades of penetration and infection exist. It would be of benefit to offer a definition of infection for purposes of clarification and discussion; such a definition must be arbitrary.

It is proposed to consider systemic infection in the smuts under three heads, seedling invasion, non-sporulating infection, and sporulating infection. By seedling invasion is meant the infection produced by the penetration of the fungus into the coleoptile or mesocotyl. This invasion of the host does not seem to affect the mature plant adversely under the conditions of germination described here. Under non-sporulating infection one may consider the "latent infection" of Zade (35), and blasting as shown by Reed and Stanton (26). It seems that here the fungus has penetrated much further than in the seedling invasion so that the host is adversely affected. However, little or no sporulation accompanies this condition. In sporulating infection, sporulation of the parasite occurs in the ovaries and their place is taken by the fungus. It is to be noted that there is no sharp line of demarcation here.

This is especially true of sportulating infection; spores may be found in parts of a spikelet, in the entire spikelet or in varying portions of the panicle.

It will be noted that this classification depends on the visible effect of the parasite on the host. It must not be assumed that causation of these different grades of systemic infection by the smut fungus is an indication of the resistance or susceptibility of the host. The environmental factors such as those demonstrated by E. S. Jones (12) and L. R. Jones (13), Reed and Faris (25), and Brandwein (4) must be carefully considered, since under environmental conditions unfavorable for infection even highly susceptible plants may not show evidence of sporulating infection. It is possible that even under favorable environmental conditions a sporulating infection will not take place, since such infection is shown only by those plants inoculated during a limited period. This period occurs early in the life of the oat seedling. Furthermore, conditions favorable for the attainment of seedling invasion must be established during this period. Yet, in highly susceptible varieties, the growing point is susceptible to a sporulating infection even in relatively mature plants. The growing points of mature plants of the resistant Markton are to all practical purposes never susceptible to a sporulating infection. This means that in Markton internal conditions in the growing point are generally unfavorable to the fungus, which cannot establish itself even if it does reach that region. All attempts by this writer to favor the fungus and inhibit the growth of the Markton host and all attempts by Reed (24) with various hosts (by different methods) failed to result in increased infection. The work of Smith and Bressman (29) is to the contrary, however.

It is apparent, therefore, that an internal factor which may be called genetic controls the stages of infection. That this is a specific property is implied in the term "physiologic race" and is supported by the work of Western (32), who shows that different races of smut penetrate to a different extent in Markton, but do not produce sporulating infection. The numerous papers of Reed (20, 21, 22, 23) and the work of Nicolaisen (18) and Reed and Stanton (26) have shown that resistance and susceptibility to various physiologic races of smut are inherited according to Mendelian laws.

This genetic factor is not to be confused with the rate of growth and maturation of the seedling. Since Monarch, Black Mesdag, and Markton exhibit remarkably similar growth rates but differ greatly in their susceptibility, it is evident that growth rates alone may not account for the ability of the plant to escape non-sporulating or sporulating infection. Von Rosenstiel (28) considers this from another viewpoint, for he finds "keine Beziehung zwischen der Lebenskraft der Haferpflanzen und dem Befall durch *U. avenae* besteht." Rapid growth may confer an apparent immunity upon any given susceptible seedling if the fungus, for one reason or another, does not enter or establish itself during the effective period of maximum infec-

tion. This helps to explain unequal infection in susceptible varieties. Markton, however, escapes infection not because of its rapid growth rate, since this does not differ from that of susceptible seedlings, but because of the operation of some internal factor.

It is apparent from the work on genetics, histology, and ecology of infection, considered with the data presented here on effective periods of infection, that there are three main factors which operate in the infection of oat varieties by a given smut fungus. These are: (1) Environmental conditions. (2) The rate of growth and maturation of the seedlings. (3) The genetic factor.

If the internal factor (genetic) and the external factor (environment) are optimum for the growth of the fungus there is a period in which the fungus must enter and develop to produce a maximum sporulating infection.

SUMMARY

The infection of various oat varieties of *Avena sativa* L. by the covered smut, *Ustilago levis* (Kell. and Sw.) Magn., has been studied under controlled environmental conditions.

1. In Monarch, a highly susceptible oat, and in Black Mesdag, a moderately susceptible variety, an effective period of infection has been found in the seedling. In Black Mesdag, this period is shorter than it is in Monarch. Similarly, the period of maximum infection appears to be longer in Monarch than in Black Mesdag.

2. The growth rates of the seedlings of Monarch, Black Mesdag, and Markton during this effective period of infection are remarkably similar. Under environmental conditions suitable for infection, the growth rate between 48 and 96 hours after planting increases approximately 480 per cent over the growth rate during the first 48 hours. In this 48–96-hour period rapidly decreasing infection percentages are found.

3. Unequal infection in susceptible seedlings may be explained on the basis of rate of growth and maturation.

4. The resistance of the Markton oat to infection cannot be explained on the basis of the growth rate. It is probably due to a specific internal factor unfavorable to the development of the smut fungus.

5. It is confirmed that inoculation with the smut fungus under the controlled environment studied here does not result in an adverse effect upon the resistant host.

6. Regional infection studies on the oat seedling indicate that while the oat smut may penetrate and develop in the mesocotyl, this invasion does not result in sporulation. The coleoptile appears to be the structure penetration of which results in highest sporulating infection.

7. It is suggested that three sets of factors control the relationship of oat

and smut fungus. They are: (1) a specific internal factor which may be analyzed on a genetic basis, (2) environmental factors, and (3) a growth factor. While the internal factor controls true resistance, the growth and environmental factors control the amount and extent of infection in susceptible seedlings.

8. The following terminology is suggested which may clarify discussion of systemic infection by oat smut:

(a) Seedling invasion. This occurs in both susceptible and resistant seedlings and need never result in sporulation.

(b) Non-sporulating infection. This appears as "blasting" or "latent" infection but does not result in sporulation.

(c) Sporulating infection. This is evidenced by a sporulation of the fungus in the fruiting structures of the host.

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TAR SPOT OF AMERICAN HOLLY

E. S. LUTTRELL[1]

(WITH SIXTEEN FIGURES)

INTRODUCTION

In 1938 Wolf and his associates (14) reported the occurrence in the Duke Forest of a tar spot disease on the foliage of American holly, *Ilex opaca* Ait., casued by a fungus commonly called *Macroderma Curtisii* (B. & Rav.) v. Höhn., and suggested that this disease deserved special study since it has not been dealt with previously. Such a study was undertaken and the results are recorded herein. Besides providing a description of the disease, the purpose of this paper is to present an account of the structure and development of the pathogen which will aid in determining its systematic position and at the same time extend the present knowledge of developmental morphology in the Phacidiaceae.

APPEARANCE OF THE DISEASE

The appearance of tiny yellow spots on holly leaves during late May constitutes the first symptom of the disease. At this stage the spots cannot readily be distinguished from those produced by certain sucking insects unless freehand sections of lesions are examined for the mycelium of the fungus. During early summer the yellow spots slowly increase in area. By the middle of July the central portion of each spot becomes reddish brown and the discolored area gradually enlarges until only a narrow border of yellow tissue remains. By fall the discoloration has deepened to shining black, and flat cushion-shaped stromata have developed beneath the epidermis. Frequently pairs of stromata develop in a single lesion, one near the upper surface and the other near the lower surface, and sometimes elongated boat-shaped ones form independently on the ventral surface of the midrib. By November the stromata on the upper leaf surface have attained diameters of 1–4 mm., while those on the lower surface are somewhat smaller. Differentiation of the stromata proceeds slowly throughout the winter months, and by April the orange-red apothecial discs are matured and are exposed by the rupture of the outer layers. After dehiscence the surrounding leaf tissues die as a result of desiccation, forming a buff col-

ored necrotic area which bears the exhausted stroma. These necrotic areas may finally drop out, leaving perforations. Infected leaves usually remain on the tree for the normal period of two years, the unaffected portions continuing to function, but occasionally severely infected leaves may become entirely yellow and moribund by the end of the first year or parts or all of the leaf may have died before that time. The fungus does not continue development after the infected tissue of such leaves becomes necrotic.

FIG. 1. Leaves of American holly infected with *Phacidium Curtisii*. The black stromata have been ruptured so as to expose the orange-red apothecial discs of the fungus.

RANGE AND IMPORTANCE OF THE DISEASE

The fungus known as *Macroderma Curtisii* is limited to a single host species, *Ilex opaca*. It has been collected in many parts of North Carolina from the sea coast to the mountains, under a wide range of environmental conditions. Collections have also been made in Virginia, Maryland, and South Carolina. There are specimens in the Farlow Herbarium from Massachusetts, Maryland, West Virginia, North Carolina, Georgia, and Florida. It seems likely, therefore, that the range of this fungus coincides with that of the American holly.

Trees of all sizes are attacked by the tar spot fungus, the age of the tree making little difference in severity of attack or freedom from disease. As a rule there is no premature defoliation. Nevertheless, infection results in a decrease in photosynthetic area of the leaves. This impairment in photosyn-

thetic tissue has not been observed to be of consequence on mature trees although it may cause a significant decrease in vigor of severely infected seedlings.

STRUCTURE AND DEVELOPMENT OF THE PATHOGEN

Development of the fungus was followed in free-hand sections cut from infected tissues supported in pith. The sections were mounted in water or in lacto-phenol in which 0.6 per cent cotton blue had been dissolved. Such preparations proved to be superior to paraffin sections for studying the morphology and host relations of the fungus, but microtome sections were necessary for determining cytological details. At appropriate intervals throughout the year fixations of infected tissues were made with Navashin's fluid, alcohol-acetic solution, or a fixative made of 4 parts of a saturated solution of picric acid in dioxan, 1 part of acetic acid, and 4 parts of absolute alcohol. The last solution gave satisfactory results and proved very convenient, since the material could be quickly passed from the fixative through several changes of pure dioxan into paraffin. Storage in dioxan did not seem to be harmful to the tissues. After the material was embedded in paraffin, sections were cut 5 μ thick. The sections were stained either with a combination of safranin followed by fast green in clove oil or with Haidenhain's iron alum haematoxylin counterstained with aqueous safranin or orange G in clove oil.

The stroma. Cross sections of the lesions found in early summer show that the host cells from the upper to the lower epidermis are occupied by mycelium of the fungus, which is entirely intracellular. The hyphae, which are about 3 μ in diameter and consist of thin-walled cylindrical cells with prominent nuclei, branch and coil within the host cells and readily penetrate the cell walls. Even vascular cells are occasionally penetrated. The infected cells, however, are not killed. The presence of the reddish discoloration in lesions during July is indicative of the initiation of stromata. Formation of the stroma is first evident within the cells of the upper epidermis. The lateral

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Explanation of Figures 2–7

FIG. 2. A portion of the hymenium of *Phacidium Curtisii* with asci in various stages of development.

FIG. 3. A section of a holly leaf bearing fertile stromata on both upper and lower surfaces. Each stroma contains a single apothecium which is exposed when the overlying stroma ruptures.

FIG. 4. A section of a leaf showing stromata within which apothecia have just begun to form.

FIG. 5. An enlarged view of a stroma before the formation of the apothecium has begun. Note that it is differentiated into dark-colored, compact basal and outer portions and a median loose plectenchymatous layer within which the apothecium will develop.

FIG. 6. A section of the median portion of a stroma in which a layer of erect hyphae, the paraphyses, is developing.

FIG. 7. Young asci growing up among the paraphyses.
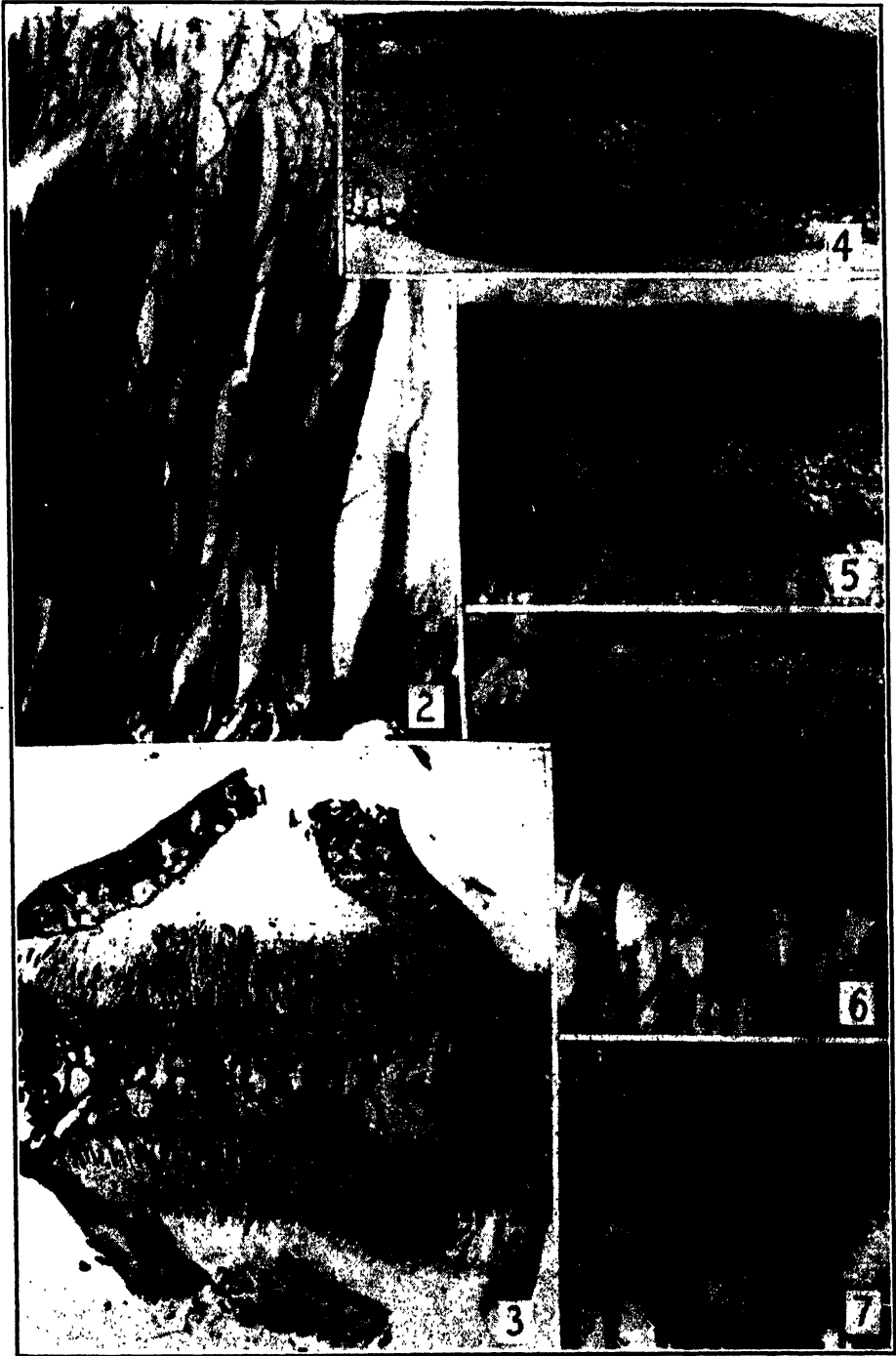
walls of these cells are ruptured and dissolved, and the mycelium forms a continuous plectenchymatous stroma in the space thus formed between the outer epidermal walls and the palisade layer. Within the central part of the infected area the palisade cells are gradually disintegrated until the stroma extends down to the spongy mesophyll. The stromata contain large druses of calcium oxalate which were formed within hypertrophic epidermal and mesophyll cells (fig. 8). A few such crystal-bearing cells are always found scattered throughout healthy leaves, but as a result of infection an inordinate number of these cells is produced. During fall the stromata become differentiated into three layers (figs. 4, 5) : (1) An outer layer in which the hyphae are thick-walled and very compactly arranged; this tissue and the adjacent epidermal walls become impregnated with a dark purplish pigment which is responsible for the deep black color of stromata when observed macroscopically, and the cuticle over these areas takes on a yellowish hue. (2) A median layer composed of a loose plectenchyma of hyaline hyphae. (3) A basal layer made up of partially disintegrated mesophyll cells filled with thick, dark-colored hyphae.

The hypophyllous stromata are formed in the same manner within the lower epidermis and adjacent spongy mesophyll. Less disintegration of leaf tissue accompanies their formation, however, because they are smaller and because of the large proportion of intercellular spaces in the spongy mesophyll. Moreover, the dark basal layer of the stroma is mostly lacking. The presence of stromata is accompanied by an increase in thickness of the infected areas, which usually become almost twice as thick as normal portions of the same leaf. Just prior to formation of the apothecia the hypophyllous stromata may be about 200 μ in thickness, while those on the upper surface of the leaf are approximately 300 μ thick.

The spermogonia and archicarps. Spermogonia mature during the latter part of August but do not occur in all stromata. They are visible macroscopically as brilliant red spots, one centrally situated on each stroma. In

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Explanation of Figures 8–16

FIG. 8. Diagrammatic drawing showing the positions of the spermogonium and the archicarps in the stroma of *Phacidium Curtisii.* The stroma has not yet differentiated into the three layers found in later stages. The large druses included in the stroma were formed within hypertrophic host cells.

FIG. 9. A section of the spermogonium showing the formation of spermatia.

FIG. 10. Archicarps of *Phacidium Curtisii.*

FIG. 11. The origin of the asci from binucleate cells located in the stroma beneath the hymenium.

FIG. 12. Mature ascospores.

FIG. 13. Stages in the formation of ascospores.

FIG. 14. Ascospore discharge.

FIG. 15. An empty ascus showing at the apex the pore through which the ascospores emerged.

FIG. 16. Germinating ascospores.
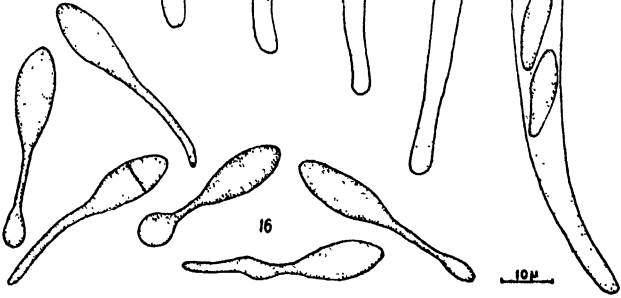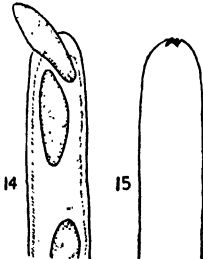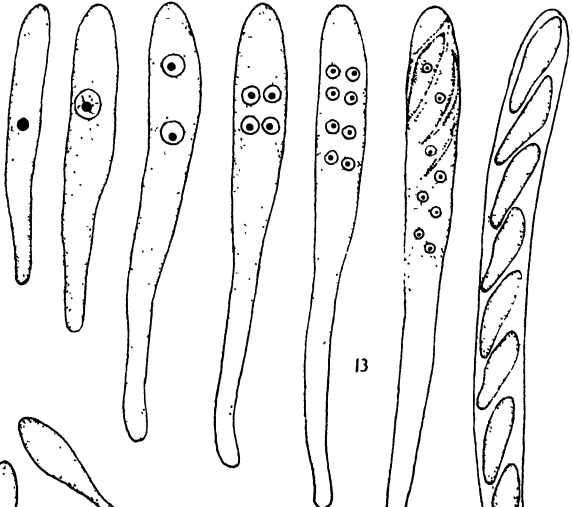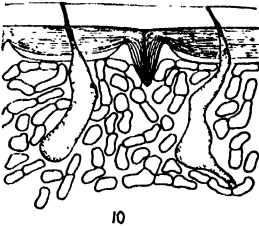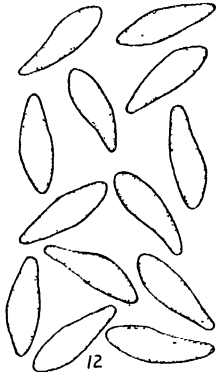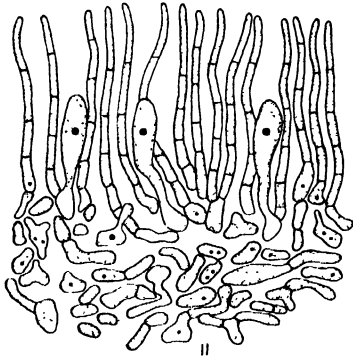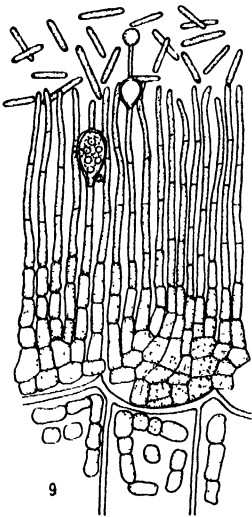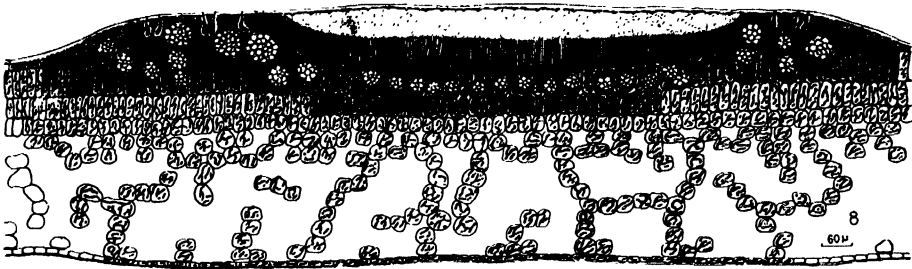
cross section the spermogonium appears as a flat, saucer-shaped structure in the outer layer of the stroma, covered only by the outer epidermal walls and leaf cuticle (fig. 8). It is therefore acervular in structure. The basal portion of the spermogonium is composed of a pseudoparenchymatous layer of polygonal cells from the surface of which arises a palisade of slender erect hyphae, the spermatiophores. They are about 40 μ long and 1.3 μ in diameter (fig. 9). Bacilliform spermatia, 7–12 × 1.3 μ, are abstricted from their tips. Interspersed among the spermatiophores are erect hyphae in which are intercalated large spherical cells (fig. 9) which are thick-walled and contain numerous refractive globules. A single hypha may contain only one of these enlarged cells, or several may be disposed at intervals along the apical portion. The function of these hyphae is uncertain, but they probably represent paraphysoid elements. When the spermogonium is mature the area between the tips of the spermatiophorés and the outer epidermal walls of the leaf is filled with a mass of spermatia.

In the same stroma, beyond the periphery of the spermogonium, deeply staining filaments that project through the cuticle may be found (fig. 8). These filaments have been traced downward through the epidermal walls and into the plectenchyma of the stroma, where each swells into an elongated bulbous structure which is non-septate and contains several nuclei (fig. 10). This structure is interpreted as an archicarp, composed of an enlarged ascogonial portion which tapers above into an elongated trichogyne. It is approximately 40 μ long and ranges in diameter from 0.3 μ at the tip of the trichogyne to 7 μ in the basal part of the ascogonium. Numerous archicarps are found in each stroma. Sometimes hyphal branches are seen to arise from the base of the ascogone and penetrate the stroma, but it has been impossible to trace them farther. Apparently archicarps develop only in conjunction with spermogonia, for in those stromata which lack spermogonia they have not been observed.

When spermogonia and archicarps first appear, the stroma shows little differentiation. Gradually the upper portions containing the archicarps become more compact and darker colored, and the archicarps disintegrate. Meanwhile the exhausted spermogonium becomes filled with a mass of plectenchyma which cements the epidermal cell walls to the stroma, and the whole structure becomes heavily impregnated with purplish pigment.

The apothecium. The apothecia are formed within the plectenchymatous median portion of the stromata. Sections of the stroma made in early March show a layer of erect hyphae, the paraphyses, developing within the plectenchyma (figs. 4, 6). The paraphyses, which arise as branches from the hyphae of the stroma and are from the first free at the tips, press against the overlying stromatic layer and by their continued growth split it in a plane parallel to the surface. When they have reached a length of about

40 μ, young asci begin to push up among them from the hypothecial layer
(fig. 7). The asci originate directly from binucleate cells in the hypo-
thecium. Each binucleate cell produces a protuberance on the side toward
the hymenium. Meanwhile the two nuclei fuse within the cell and the fusion
nucleus migrates into the protuberance, which elongates to form the ascus
(fig. 11). In early stages a large nucleolus is the conspicuous part of the
nucleus (fig. 13), while later the rest of the nucleus becomes more evident,
appearing as a hyaline area around the nucleolus.

The ascus remains uninucleate until it reaches a length of 60–80 μ. The
first division of the nucleus is oriented parallel to the longitudinal axis of
ascus, so that the two daughter nuclei are located one above the other. These
the divide in a plane perpendicular to the plane of the first division to
form four nuclei arranged in pairs, and the four nuclei divide to form
eight, likewise arranged in pairs one above the other in the ascus. Cleavage
furrows now appear in the cytoplasm surrounding the nuclei and cut out
the ascospores. Cleavage may be initiated first at the apex of the ascus and
progress towards the base, or it may delimit first the spores at the basal end.
The spores increase in size at the expense of the epiplasm until, when mature,
they measure $19–24 \times 5–6$ μ and are hyaline, one-celled, and narrowly obovate
in shape (fig. 12). When first delimited they are more or less biseriately
arranged, but they are always imbricately uniseriate by the time the ascus
is mature (fig. 13).

The ascus is cylindrical, $100–160 \times 9$ μ. The upper part, containing the
spores, is slightly enlarged, while the basal portion tapers into an elongated
stalk in which the cytoplasm is sparse and vacuolate (fig. 2). At maturity
the ascus ruptures at the apex, and the ascospores are expelled through the
irregular pore (figs. 14, 15). Asci in all stages of development may be found
in each apothecium (fig. 2). The asci, paraphyses, and cells of the hypo-
thecium become filled with golden-orange oil globules which are responsible
for the brilliant orange-red color of the disc as seen macroscopically.

At about the time that the first ascospores are mature the overlying por-
tion of the stroma is ruptured, and the hymenium is exposed (figs. 1, 3).
Dehiscence consists of a mechanical splitting resulting from the pressure
exerted by the expanding hymenium. The first evidences of dehiscence are
visible macroscopically about the middle of March, when an irregular crack
may appear across the surface of the stroma. From this crack fissures radiate
towards the margin of the stroma and deepen until the outer layer of the
stroma is completely severed. The ruptured stromatic tissue is turned back
by the expanding asci and remains as a fringe of irregular teeth bordering
the apothecium. These teeth are hygroscopic, closing over the hymenium when
dry and opening when moist to expose it again.

Ascospore germination. Ascospores for use in studies on germination were obtained by arranging leaves bearing fully developed apothecia so that the ascospores were discharged upon an agar plate or into a drop of distilled water on a glass slide.   The ascospores germinate within 12 hours by the production of a single germ tube about 1.5 µ in diameter, usually from the more acute end of each spore (fig. 16). Occasionally the ascospore may be divided into two cells by the formation of a transverse wall. In culture the hyphae do not become septate, and after reaching a length of about 25 µ they cease to grow, their tips usually swelling to form spherical vesicles. Further development in culture has not been obtained.

TAXONOMY OF THE PATHOGEN

The pathogen was originally described by Berkeley and Ravenel (North Am. Fungi no. 780) as *Rhytisma Curtisii*. Their description (8) was, however, inadequate. In 1916 Theissen (10) supplied a more complete description of the fungus, and stated, moreover, that it should not be retained in the genus *Rhytisma* because of several important differences. He noted that in other species of *Rhytisma* the ascospores are long, thread-like, and septate, and the apothecia are grouped within the stromata, while in *Rhytisma Curtisii* the spores are unicellular and elliptical and each stroma contains only a single apothecium. Although he did not make any change in name, Theissen suggested, on the basis of the characters just enumerated, that this fungus might better be placed in the genus *Phacidium* but might be found to belong to *Trochilla*.

In 1917 von Höhnel (3), without emendation of Berkeley and Ravenel's description, designated *Rhytisma Curtisii* as the type of a new genus, *Macroderma*. At the same time he divided the order Phacidiales into five families based entirely on the position of the ascocarp within the host tissue. *Macroderma* was placed in his family Dermopeltinaceae, which included those Phacidiales which develop within the epidermis. *Phacidium,* on the other hand, was placed in the Phacidiaceae, a family composed of those Phacidiales which develop beneath the epidermis or more deeply within the host tissue.

Von Höhnel's erection of the new genus, *Macroderma,* has been criticised by Nannfeldt (7, pp. 240–241), who was able to find only slight differences between *Macroderma Curtisii* and *Phacidium lacerum* Fr., the species which von Höhnel had selected as the type of *Phacidium.* He found that *M. Curtisii* differs from *P. lacerum* in the following respects: the stromata of *M. Curtisii* are larger and more strongly developed, stromata occur on the lower as well as the upper surface of the leaves, and the tips of the asci do not stain blue with iodine. He provisionally treated *Macroderma* as a separate genus, being extremely doubtful whether there is any sharp boundary between it and *Phacidium.*

Theissen (10) described the stromata of *M. Curtisii* as resting on the palisade layer which, according to him, was stained light brown but was otherwise unaffected. Von Höhnel's (3) inclusion of *Macroderma* in the Dermopeltinaceae was based on this same conception of the relation of the stroma to the host tissue. As has been shown by Nannfeldt (7) and by my own studies, however, formation of the stroma always involves more or less disintegration of the mesophyll tissues, and the stroma usually extends to the spongy mesophyll. If von Höhnel's key is followed the fungus must therefore be placed in the Phacidiaceae, where it falls naturally into the genus *Phacidium*.

The above mentioned differences between *Macroderma* and *Phacidium* do not seem to me to be of sufficient importance to warrant their separation. In other more fundamental characters they agree closely. In both *Phacidium* and *Macroderma* the apothecia are produced singly within separate stromata which are embedded in the host tissue. At maturity they are exposed by the stellate rupture of the overlying stroma and the host tissue with which it is fused. The asci are cylindrical, and the ascospores are elliptical, continuous, and hyaline. The paraphyses are slender and unbranched. *Macroderma Curtisii* is therefore transferred to the genus *Phacidium*, family Phacidiaceae. Since no adequate diagnosis has previously been published, the description is emended as follows:

Phacidium Curtisii (B. & Rav.) Luttrell, comb. nov. amend. *Rhytisma Curtisii* B. & Rav. North Am. Fungi no. 780. *Macroderma Curtisii* (B. & Rav.) v. Höhn. Ber. Deutsch. Bot. Gesel. **35**: 422. 1917.

Stromatibus in maculis innatis, planis vel discoideis, 1–4 mm. diam., atronitidis, intraepidermalibus atque foliorum in cellulis aliis; ascomatibus in verno stromatibus innatis, solitariis, amphigenis, demum irregulariter vel rimose laceratis; disco rubro-aurantiaco, 1–4 mm. diam.; ascis clavato-cylindraceis, ex hypothecio hyalino oriundis, octosporis, 110–160 × 9 μ; paraphysibus filiformibus, simplicibus, 100–160 × 1.3 μ; ascosporis oblique mono-stichis, fusoideis vel obovatis, continuis, hyalinis, 19–24 × 5–6 μ.

In aestate et in autumno spermogoniis atque carpogoniis efformantibus; spermogoniis erumpentibus, planis, miniatis; spermatiophoris simplicibus, interdum nodosis, 40 × 1.3 μ; spermatiis bacilliformibus, hyalinis, 7–12 × 1.3 μ.

Habitat in foliis vivis *Ilicis opacae*.

DISCUSSION

Apparently the Phacidiaceae are a group whose members exhibit more or less reduction in sexuality from forms which produce functional spermatia and archicarps. Higgins (2), in a study of several species of *Coccomyces*, found within the stromata archicarps, each of which consisted of a coiled ascogonial portion of enlarged uninucleate cells and an elongated trichogyne extending through the acervulus in which microconidia were produced. In a subsequent investigation of one of these species, *C. hiemalis* Hig-

gins, Backus (1) was able to show that the spermatia become attached to the tips of the trichogynes. Although actual passage of the spermatial nucleus down the trichogyne and the production of ascogenous hyphae by the ascogonial cells were not observed, it is highly probable that in *Coccomyces* fusions between spermatia and trichogynes accomplish fertilization and are a necessary preliminary to the development of asci. Archicarps similar to those of *Coccomyces* were described in two species of *Diplocarpon* by Wolf (13). The trichogynes were found to extend between the epidermal cells of the host and to develop at the same time that microconidia appeared in greatest abundance in the acervuli. It seems likely, therefore, that in *Diplocarpon* the processes of fertilization and formation of asci are the same as in *Coccomyces*.

In *Rhytisma Acerinum* (Pers.) Fr. (Jones 4), *Lophodermium hysterioides* (Pers.) Sacc. (Likhité 6), and *Phacidium repandum* Alb. et Schw. (Satina 9), the asci are produced parthenogamously. Fertilization always results from fusions between cells of a multicellular archicarp brought about by dissolution of the transverse walls. Spermatia are produced by *R. Acerinum,* but they are non-functional, the 5–6-celled archicarps being formed later and being deeply buried within the stroma. In *L. hysterioides* the archicarps, which also are completely immersed in the stroma, consist of as many as 40 cells, and no spermatia are produced. In *P. repandum,* on the other hand, the coiled basal portions of the archicarps terminate in elongated trichogynes which extend through stomata of the host, but there are no spermatia and the trichogynes are believed (9) to be functionless.

In *Lophodermium pinastri* (Schrad.) Chev., Jones (5) encountered a more complex situation. Among the spermatiophores, which are formed in acervuloid spermogonia beneath the partially disintegrated epidermis, he found bulbous, non-septate structures tapering at the apices into elongated beaks which he interpreted as receptive female organs. He found that the spermogonia later may be converted into apothecial stromata, and the ascogenous hyphae found in these stromata he considered to be derived from the above-mentioned archicarps after spermatiation. He discovered, however, that other apothecial stromata could arise independently of spermogonia and that in these stromata no archicarps were formed. Jones concluded that the ascogenous hyphae in the latter stromata originated from fusions between vegetative hyphae.

As has been shown in this paper, practically the same phenomena which Jones describes in *L. pinastri* are found in *Phacidium Curtisii.* My interpretation of the facts, however, deviates in some respects from that of Jones, for it seems unlikely that a single fungus would exhibit such diverse sexual phenomena as he indicated for *L. pinastri.* If apothecia may be produced in some stromata without the intervention of spermatia and archicarps, it is difficult to believe that these organs are essential in any stroma. Although

archicarps and spermatia are commonly present in *P. Curtisii,* they have not been demonstrated to be functional, and from the evidence now available it is concluded that the ascogenous cells always arise by some pseudomictic process from undifferentiated hyphae of the stroma.

Early in the development of the apothecium in *Phacidium Curtisii* a layer of paraphyses is formed across the median portion of the stroma. The paraphyses arise as hyphal branches which are from the beginning free at the tips, and the asci later grow up among them from the hypothecium. The hymenium therefore consists of asci and true paraphyses. The development of the apothecium is exactly like that in *Lophodermium Berberidis* (Schleich.) Rehm as described by Nannfeldt (7, pp. 234–236). Jones' (4) account of apothecial formation in *Rhytisma Acerinum* is, however, slightly different. According to this author the archicarps of *R. Acerinum* are formed within a layer of vertical hyphae in the interior of the stroma. Later these hyphae break away from the overlying stroma and cannot be distinguished from the true paraphyses which grow up among them from the stroma beneath. Nannfeldt (7, p. 217) has questioned the occurrence of true paraphyses and interthecial threads in the same hymenium, and he is supported by the present observation on *Phacidium Curtisii.*

The rupture of the outer part of the stroma in the Phacidiaceae may be caused by mechanical pressure of the expanding hymenium within, or this process may be assisted by specialized opening mechanisms in the roof of the stroma. In *Phacidium Curtisii* as in *P. repandum* (Satina 9), *Diplocarpon* spp. (Wolf 11, 12), and *Coccomyces* spp. (Higgins 2), no specialized means of opening is found. In *Rhytisma Acerinum* and in *Lophodermium pinastri,* on the other hand, Jones (4, 5) reports the presence of structures which function in the splitting of the stroma, and Nannfeldt (7, pp. 219, 235, 238) described similar mechanisms in several other species of *Lophodermium.*

SUMMARY

A tar spot disease is common on the leaves of *Ilex opaca* Ait. in North Carolina, and apparently is found throughout the range of the tree. The disease produces yellow lesions which become necrotic by the end of the first year, but the unaffected parts of the leaves usually continue to be functional for the normal period of two years. Infection results in a decrease in photosynthetic area which may affect the vigor of seedlings.

On the basis of its structure and development the pathogen, first called *Rhytisma Curtisii* B. & Rav. and later *Macroderma Curtisii* (B. & Rav.) v. Höhn., is transferred to the genus *Phacidum,* family Phacidiaceae, and the description is emended.

The mycelium of *P. Curtisii* is at first entirely intracellular. Later it forms a plectenchymatous stroma in the space resulting from a partial dissolution of the epidermal and adjacent mesophyll tissues.

The black, disc-shaped stromata are formed singly on the upper surface of each lesion, or in pairs, one on the upper and one on the lower leaf surface. During fall archicarps and acervuloid spermogonia are formed within some of the stromata. They have not, however, been demonstrated to be functional. In spring a layer of paraphyses develops across the median portion of the stroma, and the asci subsequently grow up among the paraphyses from the hypothecium. They arise directly from binucleate ascogenous cells which probably have a pseudomictic origin.

The covering layer of the stroma and the outer epidermal cell walls with which it is fused are split in a stellate manner as a result of the pressure exerted by the expanding hymenium, and the ruptured tissues remain as a peripheral fringe of hygroscopic teeth around the orange-red apothecial disc. The ascospores, which are discharged through an irregular pore in the apex of the ascus, germinate readily, forming short germ tubes, but further growth in culture was not obtained.

Development of *P. Curtisii* accords in essential features with that of other members of the family Phacidiaceae.

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TEGILLUM, A NEW GENUS OF THE UREDINALES[1]

E. B. Mains

(WITH SEVEN FIGURES)

In 1936, the writer collected a rust on a species of *Vitex* in the El Cayo district of British Honduras. This has pycnia, uredinia, and telia. The telia contain one-celled, hyaline, sessile teliospores borne in groups on laterally free sporogenous cells. The urediniospores are angular with the pores in the angles. Both the uredinia and telia are bordered by dark brown paraphyses. The genus *Olivea* is immediately suggested and specifically *O. scitula* described by Sydow (1937) on *Vitex Cienkowskii* from Sierra Leone. However further study revealed several important points of difference.

The genus *Olivea* was proposed by Arthur (1917) with *O. capituliformis* (Henn.) Arth. as the type species on *Alchornea* sp. He also described *O. Petitiae* on *Petitia domingensis*. Sydow (1937) has added a third species, *O. scitula* on *Vitex Cienkowskii*.

In his description of the genus Arthur (1917, 1925) states that the aecia are subepidermal and that the other sori are subcuticular. The aecia are described as deep seated in the host tissue and without peridia; the uredinia as minute, from stem-like bases expanding into globose masses of paraphyses. It is stated that the teliospores are one-celled, cylindric, and colorless.

Dietel (1924) differs in his interpretation of the genus in that the uredinia and telia are considered to be subepidermal and the teliospores arise in groups from fertile hyphae.

Through the kindness of G. B. Cummins and H. Sydow, I have been able to study collections of the three species. The following conclusions have been reached. The pycnia, which are known only for *O. capituliformis*, are subcuticular. The aecia, which are known only for *O. capituliformis*, are subepidermal. Their deep-seated position is due to the pronounced enlargement of the epidermal cells which overlie and surround them. The uredinia and telia, which occur in all three species, are superficial. It is difficult to determine the exact manner of their development. They appear to originate from compact masses of mycelia in the substomatal intercellular spaces. The hymenial cells probably emerge through the stomata, obliterating them. The uredinia and telia therefore develop mostly above the epidermis, the encircling peripheral paraphyses from the narrow bases producing the characteristic superficial, basket-like sori.

The rust from British Honduras shows several important points of difference. All the sori from the gametophytic mycelium (pycnia, uredinia,
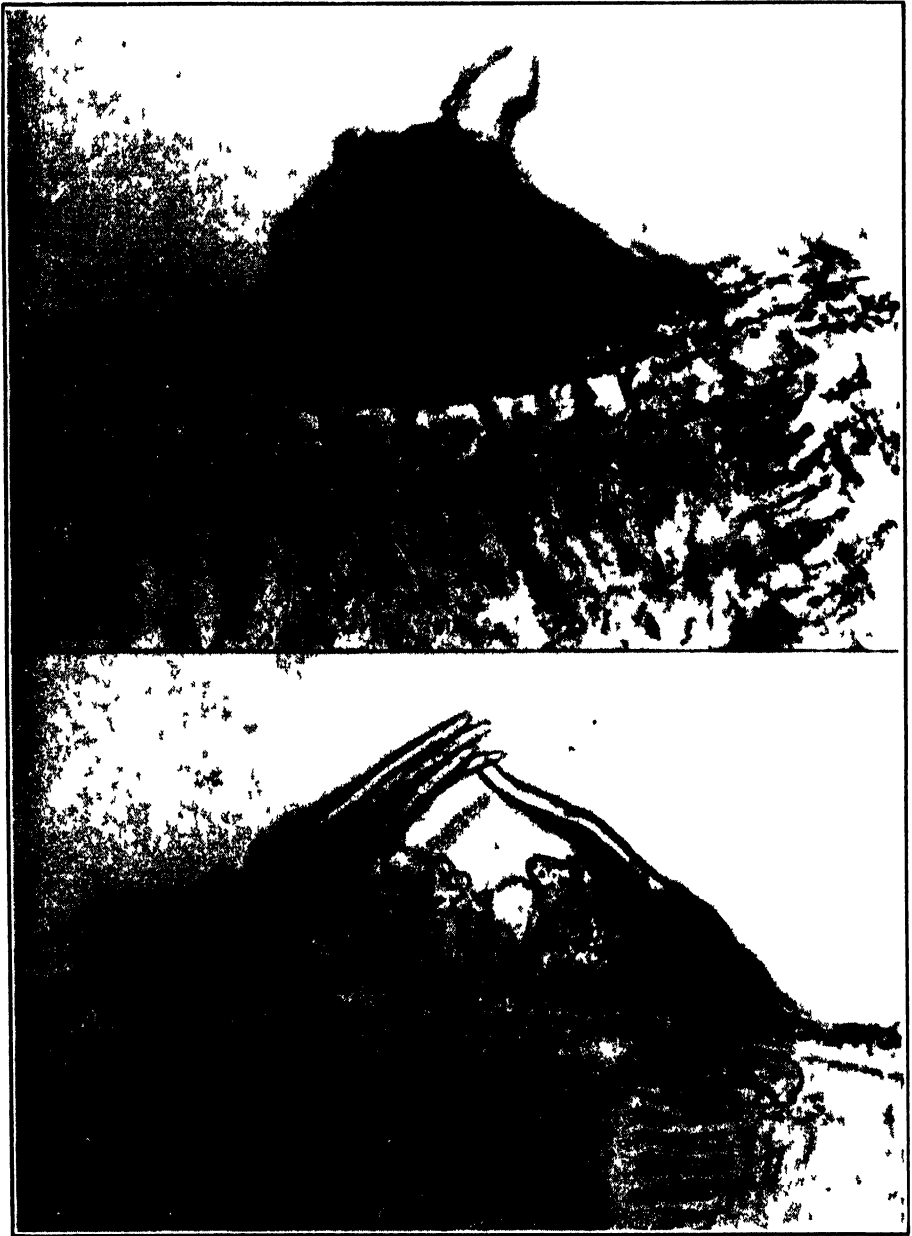
FIG. 1. Section through subcuticular pycnium, showing epidermal cells below, × 500.
FIG. 2 Section through subcuticular primary uredinium, showing overarching para
physes, × 500.

and telia) are definitely subcuticular (figs. 1–3). The uredinia from the sporophytic mycelium are subepidermal (fig. 5). In cross section the sori from the gametophytic mycelium are triangular with broad bases.

Sydow (1937) has described a genus *Desmotelium* based on *D. coaetaneum*. He states that the pycnia, uredinia, and telia are all subcuticular. He places *Desmotelium* close to *Olivea* and *Chaconia*. The uredinia are described as bordered by paraphyses and the teliospores are given as onecelled, hyaline, and occurring in groups from basal cells. Through the kindness of H. Sydow, I have been able to study the type collection and find that all the sori are subepidermal. The cells of the epidermis of the host are thin-walled and are usually crushed by the developing sori. The uredinia are very broad with a flat hymenium bordered by paraphyses.

The collection from British Honduras apparently belongs in a new genus for which the following name is proposed.

Tegillum Mains, gen. nov. Pycnia subcuticularia; prima uredinia subcuticularia, paraphysibus ad bases coalitis cincta; urediniosporae echinulatae, angulares; secunda uredinia subepidermalia; teliosporae hyalinae, membranis tenuissimis, plures ex cellula conjunctim enatae, statim germinantes.

Species typica: *Tegillum fimbriatum*.

Tegillum fimbriatum Mains, sp. nov. (figs. 1–7). Pycnia subcuticularia, amphigena, aggregata in maculis magnis, denique brunneis, late conica, 90–120 × 40–60 μ.

Prima uredinia subcuticularia, late conica, plerumque epiphylla, aggregata cum pycniis, minuta, 0.1–0.3 mm. lata, paraphysibus cincta; paraphyses cylindraceae, ad bases coalitae, membranis intense brunneis, 1.5–2 μ latis; urediniosporae turbinatae, a latere compressae, 24–30 × 20–32 μ, membranis cinnamoneis, 1 μ latis, echinulatis, poris ad angulas sitae; secunda uredinia sparsa, hypophylla, 60–100 μ lata, subepidermalia, paraphysibus pallidis.

Telia plerumque hypophylla, eadem forma et distributione quam uredinia; teliosporae clavatae vel fusoideo-clavatae, 8–10 × 30–36 μ, membranis hyalinis, 0.5 μ latis, plures ex cellula conjunctim enatae, statim germinantes.

In foliis *Viticis* sp. (*Gaumeri* ?), San Agustin, El Cayo, British Honduras, VII, 24, 1936, E. B. Mains (*3881*, specimen typicum).

Pycnia subcuticular (fig. 1), amphigenous, grouped in large spots which finally become brown, broadly conical, 90–120 × 40–60 μ.

Primary uredinia subcuticular (fig. 2), broadly conical, mostly epiphyllous, grouped in large spots with the pycnia, small, 0.1–0.3 mm., bordered and mostly covered by the paraphyses except for an irregular central opening; paraphyses cylindric, often narrowing upward, with walls dark brown, 1.5–2 μ thick coalescing at their bases to form a short pseudo-peridium (fig. 4); urediniospores asymmetrical (figs. 6, 7), turbinate but laterally compressed and therefore broadly triangular, 24–30 × 20–32 μ, from one view, the upper side sometimes protruding upward into a fourth angle, ellipsoid or obovoid, 10–18 μ wide from the other view, with the walls 1 μ thick, cinnamon-brown, finely echinulate, with the pores in the angles; secondary

FIG. 3. Section through telium, × 500.
FIG. 4. Paraphyses from a membranous base, × 500.
FIG. 5. Subepidermal secondary uredinium, × 500.
FIG. 6. Urediniospore from two views, rotated slightly less than 90 degrees, × 1000.
FIG. 7. Urediniospore from two views, rotated 90 degrees, × 1000.

uredinia subepidermal (fig. 5), very small, 60–100 µ wide, hypophyllous, scattered mostly along margins of the leaves; paraphyses light colored, cylindric, incurved; urediniospores like those of the primary uredinia.

Telia mostly hypophyllous (fig. 3), grouped in spots with the pycnia and primary uredinia, similar to the primary uredinia; teliospores one-celled, clavate or fusoid-clavate, 8–10 × 30–36 µ, with the walls hyaline, very thin, 0.5 µ, occurring in groups (7 or more) from laterally free basal cells, germinating immediately.

On leaves of *Vitex* (probably *Gaumeri*) Gracie Rock, Sibun River, British Honduras Aug. 10, 1935, Percy H. Gentle (1756); San Agustin, El Cayo, British Honduras, E. B. Mains, July 23, 1936 (3775), July 24, 1936 (*3881*, type), Aug. 4, 1936 (4058).

The gametophytic mycelium forms a large spot, apparently gradually spreading outward from the original infection. As the infection ages, the spots turn brown. Pycnia are produced at the centers of the spots, and are followed by uredinia. Teliospores probably replace urediniospores in some of the uredinia, but as the infection ages telia are produced. The uredinia are bordered by paraphyses which slope inward and upward, covering the sori except for an irregular, central, pore-like opening. In section they appear triangular with their bases on the epidermal cells. The urediniospores are unusual in shape. Only a few secondary uredinia were seen. These are very small and subepidermal. All the telia seen were from gametophytic mycelia. Telia arising from the sporophytic mycelium will probably be subepidermal and resemble secondary uredinia.

Tegillum apparently belongs in the Oliveae of the Pucciniaceae of Dietel's classification (1928). The angular urediniospores, and hyaline, one-celled, clumped teliospores, both kinds developed in sori bordered by paraphyses, indicate a fairly close relationship to *Olivea* and *Desmotelium*. It differs from both in the position and development of sori from the gametophytic myeclium.

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CHARACTERS FOR THE CLASSIFICATION AND IDENTIFICATION OF VARIETIES OF CAPSICUM[1]

H. L. COCHRAN

(WITH SIX FIGURES)

The Solanaceae contain several members on which studies have been made to determine the usefulness of various characters in the identification and classification of varieties. Salman (1924) used the leaf index for the identification of potato varieties and concluded that if certain precautions are used this character is constant for a given variety and remains so over a rather wide range of environment. Krantz and Hutchins (1928) also used the leaf index as a means of identifying certain American potato varieties and in their paper call attention to the limits of its usefulness. However, their final conclusions indicate that when varieties are grown under comparable conditions, the leaf index may be a valuable addition to the other characters which are utilized for the identification of varieties and the detection of synonyms. Lindstrom (1927) and Houghtaling (1935) have made use of the fruit-shape index in their studies on the inheritance of shapes of tomato fruits.

Although most botanists have come to recognize Bailey's (1924) classification of *Capsicum* which groups all the peppers in one species, namely *C. frutescens,* with five sub-species or varietal groups, there is still occasional confusion in properly classifying some horticultural varieties. It has been the chief aim of this paper, therefore, to bring together facts that may prove beneficial in the classification and identification of such varieties of *Capsicum.*

MATERIALS AND METHODS

Plants of 59 varieties of peppers were grown to maturity in 12-inch clay pots in the greenhouse during the winter of 1937 and in the field during the spring and summer of 1938. Observations and study were made of the leaves and fruits of both crops; definite measurements, however, were taken only on plants growing under field conditions. From 20 to 100 mature leaves and fruits were selected at random over the plots for each variety and their length and width accurately measured, the readings being taken to the nearest millimeter. The index for each variety was determined by the following formula: $\dfrac{W \times 100}{L}$. W represents the average width of the leaf for the variety, while L represents the average length. The width is multiplied by 100 in order to express the result as a percentage. The fruit-shape index

was computed for each fruit by dividing the length by the width. The probable error of the mean was calculated by the following formula:

$$PE_M = .8453 \frac{\Sigma(+)d}{\sqrt{n\,(n-1)}}.$$ A typical leaf and fruit of each variety studied were outlined on paper for a record of their shape and size.

OBSERVATIONS AND DATA

From the data presented in table 1 it is seen that the leaf index varies over quite a wide range between varieties, the highest being 71.02 ± 0.68 for Sweet Meat Glory and the lowest 39.95 ± 0.27 for Minimum. As a whole, however, the index figures are higher for the mild-flavored varieties than for the pungent ones. Correspondingly in table 1, but possibly more clearly in figures 1, 2, and 3, it is to be noted that there exists an even more consistent difference between leaf sizes for the two varietal groups cited above. Almost uniformly large leaves are associated with mild-flavored varieties while small leaves are associated with pungent varieties. Further analysis of these data indicate the existence of a definite relationship between leaf size and fruit size for the varieties studied. The coefficient of correlation between leaf length and fruit length and between leaf width and fruit width was 0.364 and 0.733 respectively. Both of these values are highly significant. The correlation between leaf shape and fruit shape was 0.028.
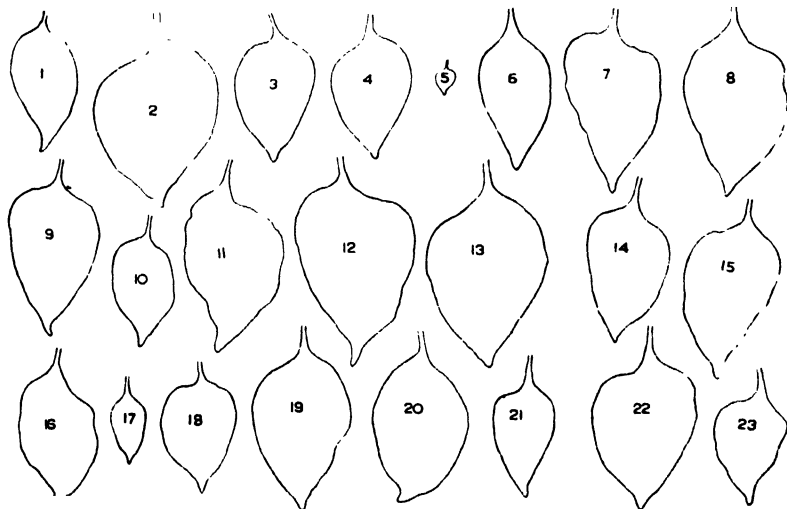
Fig. 1. Trace drawings of typical mature leaves of the varieties shown in table 1.

While no actual measurements were made of leaves from the plants of any variety growing in the greenhouse, observations indicated clearly that leaf sizes were larger under these conditions than those of the same variety growing under field conditions, the difference being due, no doubt, to a

TABLE 1

Leaf and fruit characters of 59 varieties of Capsicum

Variety number	Variety name	Average leaf length	Average leaf width	Leaf index	Average fruit length	Average fruit width	Fruit shape index	Fruit[1] flavor
		cm.	cm.		cm.	cm.		
1	Anheim Chili	8.84	4.51	51.02 ± 0.48	12.90	3.64	3.54 ± 0.06	P
2	Asgrow Calwonder	12.55	8.25	65.74 ± 0.58	10.03	8.43	1.19 ± 0.01	M
3	Asgrow King	9.01	5.67	62.93 ± 0.59	11.31	7.44	1.52 ± 0.04	M
4	Bell or Bull Nose	8.73	5.68	65.06 ± 0.56	5.98	6.78	0.88 ± 0.02	M
5	Bird's Eye	2.09	1.40	66.99 ± 0.60	0.94	0.67	1.40 ± 0.02	P
6	Burpee's Sunnybrook	9.96	5.01	50.30 ± 0.47	4.54	6.85	0.66 ± 0.01	M
7	California Wonder	11.61	6.89	59.35 ± 0.57	8.47	7.25	1.17 ± 0.03	M
8	California Wonder Bell	11.94	7.24	60.64 ± 0.48	7.75	8.11	0.69 ± 0.03	M
9	Cayenne	10.67	6.13	57.45 ± 0.52	11.39	1.43	7.97 ± 0.14	P
10	Celestial	7.77	4.26	54.83 ± 0.50	2.68	1.81	1.48 ± 0.02	P
11	Certified Florida	11.82	6.64	56.18 ± 0.54	8.23	8.10	1.02 ± 0.02	M
12	Certified Ruby King	13.00	8.31	63.92 ± 0.57	11.03	6.53	1.69 ± 0.03	M
13	Chinese Giant	12.95	8.56	66.10 ± 0.49	7.97	8.87	0.90 ± 0.06	M
14	Crimson Giant	9.75	5.95	61.03 ± 0.58	8.81	6.58	1.34 ± 0.03	M
15	Early Dwarf California Wonder	11.58	6.42	55.44 ± 0.39	8.75	7.85	1.11 ± 0.02	M
16	Early Normandie	9.80	5.25	53.57 ± 0.46	10.70	6.93	1.54 ± 0.04	M
17	Florida Gem	5.04	2.47	49.01 ± 0.40	4.58	2.79	1.64 ± 0.02	M
18	Golden Dawn	8.11	5.15	63.50 ± 0.57	8.90	5.84	1.52 ± 0.04	M
19	Giant King	11.26	6.93	61.55 ± 0.51	10.94	6.79	1.61 ± 0.05	M
20	Golden Queen	10.53	6.75	64.10 ± 0.55	9.57	7.60	1.26 ± 0.05	M
21	Green Mexican Pickling	8.09	4.39	54.26 ± 0.35	6.60	3.30	2.00 ± 0.04	P
22	Harris' Early Giant	11.05	7.37	66.70 ± 0.60	8.03	7.08	1.13 ± 0.02	M
23	Harris' Earliest	7.87	5.05	64.17 ± 0.55	8.29	5.83	1.42 ± 0.04	M
24	Harris' Wonder	10.54	7.20	68.31 ± 0.42	10.88	7.19	1.51 ± 0.04	M
25	Harris' King of the North	9.57	5.46	57.05 ± 0.39	7.68	7.17	1.07 ± 0.03	M
26	Harris' Improved Squash	11.01	6.28	57.04 ± 0.59	4.77	6.68	0.71 ± 0.01	M
27	Holmes' Prolific Sweet	9.56	6.05	63.28 ± 0.62	9.01	7.40	1.22 ± 0.03	M
28	Hot Portugal	8.32	4.57	54.93 ± 0.54	15.07	3.05	4.94 ± 0.01	P
29	Hungarian Wax	8.68	5.04	58.06 ± 0.50	13.61	3.54	3.84 ± 0.01	P
30	Hungarian Yellow	8.80	4.21	47.84 ± 0.41	12.93	3.55	3.64 ± 0.01	P

[1] M = Mild; P = Pungent.

TABLE 1—(*Continued*)

Variety number	Variety name	Average leaf length	Average leaf width	Leaf index	Average fruit length	Average fruit width	Fruit shape index	Fruit[1] flavor
		cm.	*cm.*		*cm.*	*cm.*		
31	Improved Collossal	12.65	7.53	59.53 ± 0.53	10.32	7.42	1.39 ± 0.03	M
32	Leonard's Early Wonder	10.59	5.12	48.35 ± 0.46	9.83	5.48	1.79 ± 0.01	M
33	Little Gem	4.74	2.39	50.42 ± 0.34	3.07	1.92	1.60 ± 0.02	P
34	Long Red Cayenne	9.03	4.87	53.93 ± 0.48	11.89	2.58	4.61 ± 0.09	P
35	Low Bush California Wonder	10.59	6.54	61.76 ± 0.52	8.17	7.62	1.07 ± 0.04	M
36	Long Thick Red	8.07	3.81	47.21 ± 0.39	8.83	3.17	2.79 ± 0.09	P
37	Meales Red Hot	11.40	5.48	48.07 ± 0.47	14.04	3.30	4.25 ± 0.06	P
38	Mexican Chili	8.62	5.05	58.58 ± 0.51	8.19	4.81	1.70 ± 0.02	P
39	Minimum	3.93	1.57	39.95 ± 0.27	1.76	1.06	1.66 ± 0.03	P
40	New Mexico No. 9	9.41	5.24	55.69 ± 0.41	12.95	3.44	3.76 ± 0.05	P
41	Neapolitan	7.50	4.26	56.80 ± 0.50	10.79	4.82	2.24 ± 0.06	M
42	Oshkosh	8.55	4.72	55.20 ± 0.52	6.71	7.00	0.96 ± 0.02	M
43	Paul's Jersey Giant	8.31	4.90	58.97 ± 0.63	9.08	8.22	1.10 ± 0.04	M
44	Perfection Pimiento	12.00	8.05	67.08 ± 0.57	7.18	6.32	1.14 ± 0.02	M
45	Red Chili	8.94	5.67	63.42 ± 0.52	12.65	3.35	3.78 ± 0.08	P
46	Red Oshkosh	11.56	6.42	55.54 ± 0.49	7.06	7.90	0.89 ± 0.03	M
47	Rocky Ford	10.28	5.35	52.04 ± 0.55	10.15	8.02	1.27 ± 0.04	M
48	Ruby Giant	11.37	7.42	65.26 ± 0.60	8.73	8.28	1.05 ± 0.02	M
49	Ruby King	12.75	7.45	58.43 ± 0.57	11.03	7.20	1.53 ± 0.02	M
50	Simon's World Beater	13.19	7.29	55.27 ± 0.46	10.35	7.62	1.36 ± 0.02	M
51	Squash or Tomato	10.07	6.40	63.56 ± 0.44	4.20	6.30	0.67 ± 0.01	P
52	Sport	7.24	4.41	60.91 ± 0.53	10.73	1.47	7.30 ± 0.02	M
53	Sweet Meat Glory	12.32	8.75	71.02 ± 0.68	8.88	6.46	1.37 ± 0.06	M
54	Sweet Yellow	12.21	7.24	59.30 ± 0.49	7.40	6.48	1.14 ± 0.02	P
55	Tabasco	9.05	4.61	50.94 ± 0.56	3.01	0.54	5.57 ± 0.12	P
56	Talinette	9.07	4.77	52.59 ± 0.54	14.88	4.22	3.53 ± 0.13	P
57	Waltham Beauty	11.04	6.93	62.77 ± 0.57	7.75	7.95	0.97 ± 0.03	M
58	Windsor A	9.55	6.34	66.39 ± 0.60	10.54	6.54	1.61 ± 0.03	M
59	Windsor B	8.52	4.68	54.93 ± 0.51	9.92	7.14	1.39 ± 0.02	M
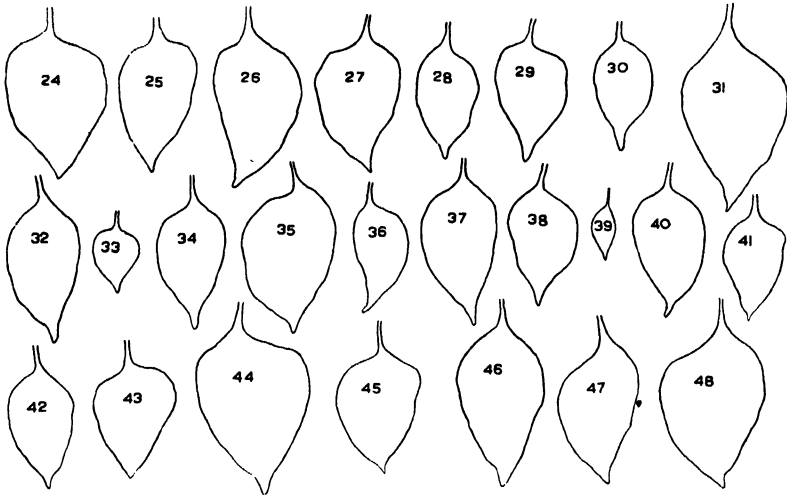
Fig. 2. Trace drawings of typical mature leaves of the varieties shown in table 1.
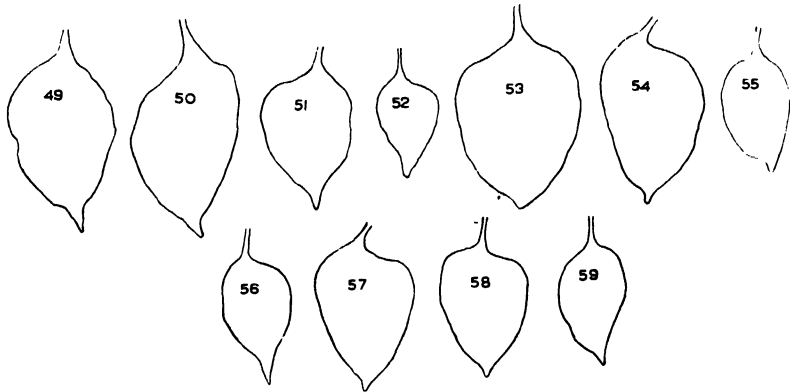
Fig. 3. Trace drawings of typical mature leaves of the varieties shown in table 1.

better growing environment in the former, and especially to moisture. Had the leaf index been computed for the varieties growing in the greenhouse, the figures obtained would have differed to some extent from those of the same variety growing in the field, perhaps as much as between some varieties. This observation is substantiated by the findings of Krantz and Hutchins (1928), who grew potatoes in several locations in the State of Minnesota and found that the environment produced significant differences in the leaf index of all varieties tested except one, which remained constant.

While measurements were being made of mature leaves from the field plots, it was rather surprising to learn of the uniformity of size among mature leaves within a given variety. Apparently the leaf index should remain rather constant for a given variety under comparable conditions.

By comparing the data in table 1, under the fruit-shape index column, with the fruit tracings of the varieties in figures 4, 5, and 6, it is evident
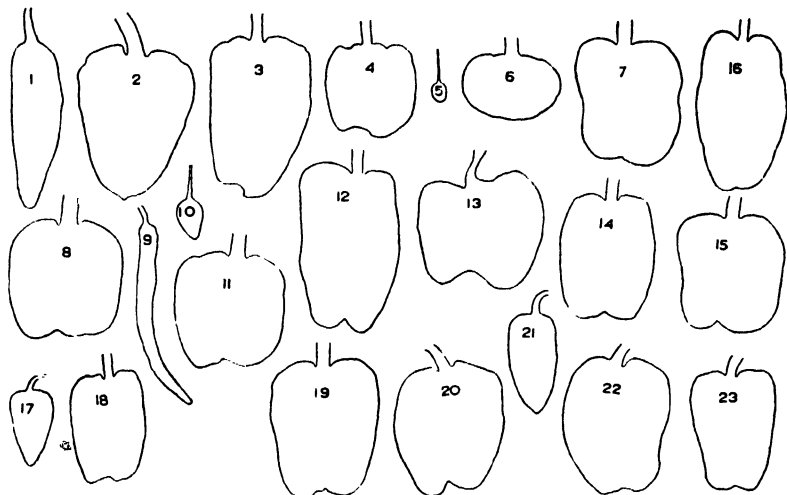
FIG. 4. Trace drawings of typical ripe fruits of the varieties shown in table 1.
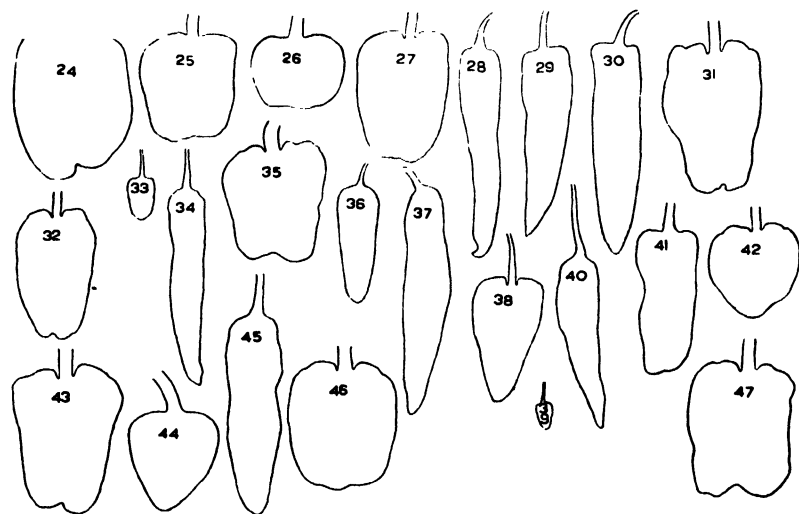
FIG. 5. Trace drawings of typical ripe fruits of the varieties shown in table 1.

that varieties may be grouped into two general classes according to fruit shape. The first group contains varieties with from blocky to almost spherical fruits having shape indices ranging from 0.66 ± 0.01 to 2.24 ± 0.06, while the second group contains long fruits of various shapes with indices ranging from 1.40 ± 0.02 to 7.97 ± 0.14. Previous observations by the writer, as well as definite measurements made during this study, show that in some varieties the shape of the ovary changes greatly between the stages
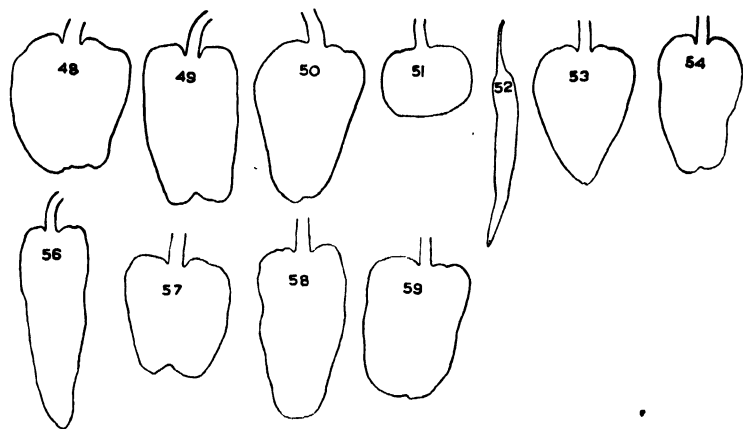
FIG. 6. Trace drawings of typical ripe fruits of the varieties shown in table 1.

of anthesis and fruit maturity. These findings agree fully with those reported earlier by Sinnott and Kaiser (1934), who showed that most shape types in *Capsicum* have fruit primordia that are essentially isodiametric at the time of flowering, but that this relation is maintained only in the spherical types until maturity. In the elongated fruit type the authors state further that a much more rapid growth takes place in length than in width. By far the most complete analysis of the above-stated change in fruit shapes in *Capsicum* has been that reported by Kaiser (1935). From his work it is evident that environmental conditions influence fruit shape to some extent but the ultimate configuration of the fruits depends on the interaction between genes which control shape development and those which govern size.

When the same varieties were grown under both greenhouse and field conditions, it was quite noticeable that fruit shapes are more easily altered by environment than are leaf shapes. Nevertheless, under the conditions of this experiment both characters proved to be relatively constant. This does not mean, however, that either could be used alone in making positive variety identifications.

<div align="center">SUMMARY</div>

Leaf and fruit measurements were made and their respective indices computed for 59 varieties of *Capsicum* grown under field conditions. Observations were made on the same varieties growing in the greenhouse. It was found that there exists a definite relationship between leaf size and fruit size but little correlation between leaf shape and fruit shape. The index figures extend over a rather wide range among varieties, as would be expected. However, the leaf and fruit index may be valuable together with certain other plant characters in the classification and identification of

pepper varieties grown under comparable conditions, but would seemingly be of little value when used alone.

The writer is indebted to Mr. Leslie R. Hawthorn of Texas Substation No. 19 at Winter Haven, Texas; to Dr. Roy Magruder of the U. S. Horticultural Station at Beltsville, Maryland; and to Dr. Paul Work of Cornell University at Ithaca, New York, for furnishing the seeds of some of the pepper varieties used in this study.

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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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THE EMBRYOGENY OF TORREYA, WITH A
NOTE ON AUSTROTAXUS

J. T. BUCHHOLZ

(WITH FORTY-FOUR FIGURES)

INTRODUCTION

Several morphological investigations of *Torreya* (Tumion) have been published, but the embryogeny, except for the proembryo, still remains to be described. Strasburger (18) described the structures found in the longitudinal sections of a pair of the ovules of *T. nucifera* (L.) Seib. & Zucc. at the time of pollination. Miss Robertson, now Mrs. Agnes Arber (12, 13, 14), has given us, in a series of three papers, all that is known concerning the special morphology of *T. californica* Torrey, which included no mention of the events in the enlargement of the ovule and the maturity of the seed in the subsequent season. Coulter and Land (5) have given similar details for *T. taxifolia* Arnott. This work included the development of the proembryo, ovule, and seed in the season after fertilization. None of the remaining three species has been investigated. Since the accounts of these two species differed somewhat with respect to the size and structure of the female gametophytes and the number of archegonia, it is surprising that no one has subjected these, or any of the other species of *Torreya*, to additional investigation.

When these accounts are compared, one finds that the male gametophytes differ considerably in their relative stages of development near the time of fertilization. Miss Robertson's figures seem to show that at the time when the female gametophyte of *T. californica* is cellular and has its archegonia showing neck cells the pollen tube has only grown about half-way through the nucellus. For *T. taxifolia*, on the other hand, Coulter and Land have shown a figure in which the pollen tube has grown the full distance through the nucellus and is in contact with the female gametophyte while the latter is still in the free-nuclear stage of development. In other words, in *T. californica* the female gametophyte is precocious in development, while in *T. taxifolia* it appears that the male gametophyte is precocious.

It was pointed out by Coulter and Land (5) that at the time of fertilization the female gametophyte of *T. taxifolia* consists of only 400 or more cells. It is, therefore, very small, only about 200×300 μ (by error given as 20×30 μ), which is somewhat smaller than *Taxus*, and very much smaller than either *Austrotaxus* (16) or *Cephalotaxus* (1, 4) at the time of fertilization, the latter being nearly 12 mm. long in this stage. It is well known that the female gametophyte of *Taxus* enlarges considerably after fertilization, but much less than *Torreya*, which has, in addition, the infolded and corrugated female gametophyte usually described (5) as a "ruminating endosperm."

Another remarkable feature is the small size of the archegonia. These are only 70×100 μ at the time of fertilization of *T. taxifolia* and there is usually only one. According to Miss Robertson's drawings the archegonia of *T. californica* are much larger, 85–90 μ $\times 180$–250 μ at the time of fertilization. The number of archegonia is usually 3 and ranges between 2 and 5. However, these sizes given for the archegonia show that they are no smaller than those of *Taxus* (7, 8) at the time of fertilization, but they are only about half the size of those of *Austrotaxus* (15) and *Cephalotaxus* (4). Miss Robertson's drawings show that the size of the female gametophyte, at a stage before fertilization with half-grown pollen tube, are 420×625 μ and, in a later stage with proembryos, they are 480×1100 μ. The female gametophyte is, therefore larger in *T. californica* than in *T. taxifolia*.

Other differences have been recorded in the archegonia. Miss Robertson (13) found four or more neck cells (she shows one instance with 6 neck cells) and mentioned the differentiation of jacket cells. Coulter and Land (5) found only two neck cells, which usually disintegrate while in intimate contact with the pollen tube long before fertilization, and they recorded no specially differentiated archegonial jacket. The ventral canal nucleus is not formed in either species, though one mitotic figure which may represent the central cell nucleus in division was observed in *T. californica*. These differences in the female gametophytes all indicate that *T. californica* is the more primitive species and *T. taxifolia* is advanced with respect to the gametophytes near fertilization. The latter species has lost many gametophytic features which are found in other conifers and are still present in *T. californica*. Pilger (11) in his monographic treatment of the taxonomy of this group places *T. nucifera* as the most primitive species and considers *T. Fargesii* Franch., *T. taxifolia*, and *T. californica* as more advanced.

MATERIALS AND METHODS

The material which the writer has obtained for a study of the embryogeny came from several sources. Material of *T. nucifera* was obtained from the New York Botanical Garden in several stages of development and in different

years, no two of them in sequence. The stages before fertilization were obtained late in August, fertilization occurred in the last two weeks of September, and proembryos were found in all subsequent collections. However, a long dormant period ensues, so that there is no great change in the stage of development of the embryo from October until May or June of the following year. The ovules which enlarge in the spring were fertilized in the preceding September.

Several embryos of *T. californica* were obtained in 1936 from specimens found in cultivation at Golden Gate Park in San Francisco and later stages from Yosemite National Park near El Portal entrance. Through the kindness of Professor W. J. G. Land, I have received a series of microscopic slides, showing the morphology and embryogeny, which came from the Coulter and Land investigation, with permisson to include them in my investigation. This material of *T. taxifolia* included gametophytes before fertilization, proembryo stages similar to those described and figured by Coulter and Land (1904), and also several later stages, all of which had been sectioned. From these materials of three species the writer is able to present a general outline of the embryogeny of this genus. There are, no doubt, many important details concerning gametophytes and embryos which have been overlooked in this general survey.

The ovules of *T. nucifera* in fertilization stages were imbedded and sectioned by the usual methods after the scales had been removed by dissection under a binocular microscope. Preliminary dissection is necessary, since the scales which cover the ovules prevent a rapid penetration of the fixative and are difficult to cut. The ovules in the enlarged stages of the following season of both *T. nucifera* and *T. californica* were dissected by the methods described elsewhere (2), while those of *T. taxifolia*, which had already been sectioned, were delineated from the sections.

<div align="center">OBSERVATIONS</div>

Torreya nucifera. Pollination had been very good, so that few ovules with healthy female gametophytes were without one or more pollen tubes. However, in 10 of 50 ovules (up to fertilization stage) one or more pollen tubes were observed with the entire absence of female gametophytes. In these the male gametophytes appeared to be normal; a month later such pollen tubes were found to be undergoing disintegration.

Figure 1 shows two archegonia of *T. nucifera* as found in the last week in August shortly before fertilization. The neck cells of the archegonia are still clearly visible and though crowded and slightly displaced in the archegonium at the right, they have not been digested by the action of the tip of the pollen tube, which, according to Coulter and Land (5), appears to arrive much earlier in *T. taxifolia* and destroys the neck cells. Many other

archegonia were observed with neck cells, including the ones shown in figures 5, 6, and 12. The number of neck cells in *T. nucifera* is usually 4 and ranges from 2 to 8. Of 42 archegonia in which the neck cells were counted, 5 had only 2, 2 had 2 or 3, 6 had 3, 1 had 3 or 4, 20 had 4, 2 had 5, 5 had 6, and 1 had 8 neck cells. These were always situated in the same plane or tier. The female gametophyte has a mean width of 260 μ and a mean length of 355 μ about a week before fertilization, has increased to 300 × 410 μ at fertilization and increases slightly during the following month up to the stage of winter dormancy.

The archegonia are usually 3 in number; only two may usually be observed in the same section. One doubtful case may have had only a single archegonium.
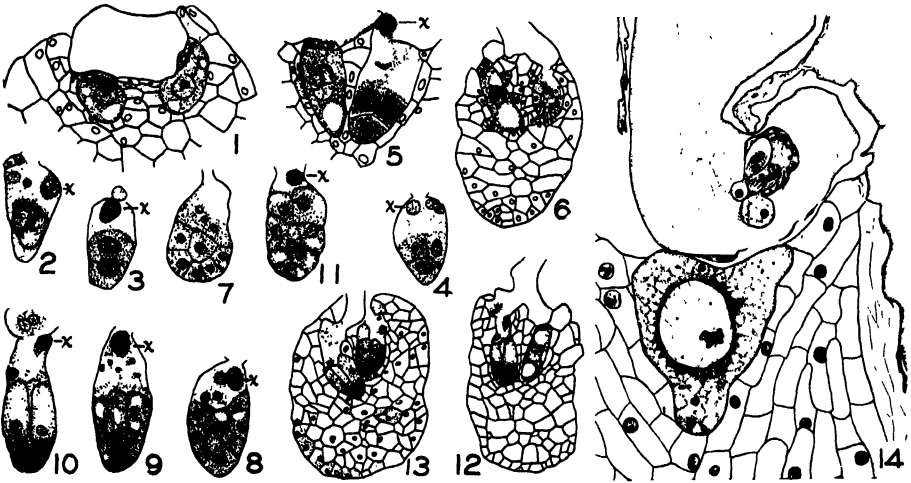
FIG. 1. Tip of female gametophyte of *T. nucifera* about September 1, before fertilization, showing two archegonia in contact with end of pollen tube. × 110. FIG. 2. Archegonium in fertilization. Male nucleus is in contact with egg nucleus with abandoned cytoplasm of male cells at *x* above, also the nucleus of smaller male cell. × 110. FIG. 3. Archegonium with proembryo in 2-nucleate stage, the abandoned male cytoplasm and smaller male nucleus showing in neck. × 110. FIG. 4. Proembryo with 4-nucleate stage, cell walls beginning to form. × 110. FIG. 5. Two adjacent archegonia, the one at left still unfertilized, the other with 4-celled proembryo, also shows the abandoned male cytoplasm *x* above neck. × 120. FIG. 6. Female gametophyte showing 2 archegonia, the one at right with proembryo. × 55. FIG. 7. Proembryo of figure 6, 10–12 celled stage; nuclei above proembryo may be smaller male nucleus, stalk, and tube nucleus. × 120. FIG. 8. 12-celled proembryo showing smaller male nucleus beside abandoned male cytoplasm, also two other nuclei which may have been derived from pollen tube. × 110. FIG. 9. A 12-celled proembryo with prosuspensors, beginning to elongate. Abandoned male cytoplasm above. × 110. FIG. 10. Similar proembryo showing elongation of prosuspensor, also male cytoplasm *x* and 3 nuclei. × 110. FIG. 11. Proembryo of 16–18 cells. × 110. FIG. 12. Section of gametophyte containing embryo of figure 10. × 55. FIG. 13. Section of female gametophyte with two proembryos resulting from the fertilization of two archegonia. × 55. FIG. 14. *T. taxifolia* showing relation of gametophytes at fertilization. In the pollen tube above at the right, the male nuclei are being discharged from the male cells. × 285.

In a count of 32 ovules with healthy female gametophytes before or at fertilization, 7 had only 2, 16 had 3, 8 had 4, and 1 had 5 archegonia. The mean dimensions of 32 young archegonia were (49.3 × 99.6 μ) very nearly 50 × 100 μ. Archegonia in fertilization and early proembryo stages were 58 × 120 μ (mean of 45 archegonia). Among those containing proembryos in which the neck region of the archegonia was more or less indefinite, the mean dimensions obtained from 24 were 74.5 × 111 μ. In many respects at the time of fertilization *T. nucifera* resembles *T. taxifolia* only in the small size of the archegonia, otherwise with respect to plurality of archegonia and neck cells it resembles *T. californica* much more closely, and in the size of female gametophytes it is intermediate.

No structure which might be described as an archegonial jacket was observed. The cells bordering archegonia are large in some places and very small in others. When large, their nuclei are sometimes correspondingly large, which may lead to the impression that a few scattered jacket cells are present. There is no indication that a ventral nucleus is formed in any of the species. Miss Robertson (12) illustrated one instance in which the mitotic figure in the formation of a ventral nucleus is suggested, but from her account this appearance must be very rare. There is no megaspore membrane. If a megaspore membrane is present, it is so thin that it cannot be distinguished from the walls of the marginal cells of the female gametophyte.

Fertilization was observed in several instances. Conditions in one of these are shown in figure 2, where the smaller male nucleus is found in intimate contact with the egg nucleus, but the nuclear membrane separating them has not disappeared. A spherical mass of abandoned cytoplasm (x) which usually stains deeply is observable at the right above the fusion nucleus. One of the nuclei at the left may be the smaller male nucleus, the other the stalk nucleus or the tube nucleus. In this archegonium 2 of 3 or more neck cells are shown at the left. Sometimes deeply staining chromidial bodies are included in this abandoned cytoplasm. These may at times include the remains of entangled neck cells. In figure 3, where dislodged neck cells are not included in the section, the cytoplasm of the male cell is also evident near the neck, and a similar smaller male nucleus is situated immediately above it. The same deeply-staining cytoplasm of the male cell x is usually found and is shown in the proembryos of figures 4, 5, 8, 9, 10, 11, and 12. The smaller male nucleus and sometimes traces of the stalk nucleus are visible in some of the sections.

The separation of the male nuclei from the cytoplasm of the male cells could not be observed in *T. nucifera*. However, in one of the preparations of *T. taxifolia* the extrusion of male nuclei was observed. A highly magnified drawing of this section is shown in figure 14, which includes the lower end of a pollen tube touching an archegonium at the time of fertilization. The

male nuclei have at the time of their extrusion the form of an hour glass. The larger male nucleus has almost completed its emergence while the smaller male nucleus is just beginning to pass to the exterior. It will be noted that the two male cells do not become separated into distinct cells, so that a common mass of the male cytoplasm of both cells is left behind; in fact this might be spoken of as the cytoplasm of the body cell. These naked nuclei pass into the archegonium while the deeply stained abandoned cytoplasm remains behind. As shown in figure 14 this abandoned cytoplasm of the male cells may remain in the pollen tube. In *T. nucifera* figure 5 shows it above the neck, figures 2, 3, 8, 9, and 10 show it inside the upper region of the archegonium, but it is clear that in no case is the abandoned male cytoplasm included in the proembryo.

The manner of extrusion of a nucleus from the male cytoplasm in its hour-glass form resembles the condition found in *Sequoia sempervirens* (3), except that·in the latter species the male cells first become separated from each other and take on a tear-drop form, with the nuclei emerging from the pointed end inserted into the necks of the archegonia.

About 28 proembryos of *T. nucifera* were observed in stages similar to figures 2–13. Figure 3 shows the 2-nucleate stage, figure 4 the 4-nucleate stage with walls beginning to form, and figure 5 the same stage with walls completed. The proembryo therefore occupies the lower half or two-thirds of the archegonium. This is in agreement with Miss Robertson's findings shown by her figures 23–26, plate 9, but appears to differ from *T. taxifolia*. This difference in the latter species is not so real as it seems, for in *T. taxifolia* the pollen tube not only destroys the neck cells, but invades and distorts the upper portion of the archegonium.

In *T. nucifera* the region occupied by the proembryo is limited to a zone of dense cytoplasm; within it is a denser zone close to the nucleus or nuclei. Actually this cytoplasmic zone is completely filled by the proembryo in all Torreyas. In *T. nucifera* and *T. californica* this denser zone of cytoplasm, and therefore the proembryo, occupies little more than half of the archegonium, while in *T. taxifolia* where the pollen tube has invaded the upper part of the archegonium this region of denser cytoplasm is the only part of the archegonium that is recognizable. Consequently, one usually finds the walls in the proembryo of the latter extending across this entire space, and this circumstance gives the impression that the proembryo fills the entire egg.

With this explanation for the apparent exception in *T. taxifolia,* the proembryo is in agreement with other Taxads and with conifers generally. It would not fill the entire archegonium if the entire archegonium were still present.

The divisions are not always regular in subsequent stages, and so give rise to the 6-celled, 8-celled and 12-celled proembryos shown in figures 7, 9,

and 10. Figures 8 and 11 seem to be embryos in a slightly later stage with 14–16 cells. In these stages the upper tier of cells or the entire proembryo elongates, soon fills the archegonium, and crowds the surrounding tissues. The proembryo becomes an arrested embryo through the late fall, winter, and early spring. I shall call this winter stage the *hibernal* embryo.

In late May or early June of the subsequent season the ovules enlarge rapidly. In ovules which had enlarged to sizes between 9 and 18 mm. long and between 6 and 10 mm. wide, the embryos were still found as hibernal embryos. Coulter and Land state that the proembryo of *T. taxifolia* remains dormant during the enlargement of the gametophyte as it develops into a ruminating endosperm. This same condition was found in *T. nucifera*. Figure 15 shows an hibernal embryo imbedded in the micropylar tip of the female gametophyte, whose upper boundary is shown by the line *m*. Figure 16 shows a similar hibernal embryo. Several others similar to these were found in a dozen gametophytes, which were successfully dissected from well-enlarged ovules. Here only two distinct tiers of cells are found if all of the shaded cells below are counted as belonging to the same tier, or there are three tiers if more than a single tier is counted in the group of cells below, whose number and arrangement is variable. These are all past the proembryo stage according to the more precise definition of the term proembryo, since some of the cells had begun to elongate before they were arrested in growth to form the hibernal stage. *Hibernal* is a term which carries the implication that they are slightly past the true proembryo stage, and remain relatively inactive throughout the late autumn, winter, and early spring. I am using the term *prosuspensor* for the group of 4 or more cells in the proembryo which elongate; these same suspensor cells are spoken of by previous investigators as suspensor or primary suspensor. Sometimes a canal or other faint line may be seen above the hibernal embryo leading upward to the nucellus. This passage marks the region above the archegonium which became closed as the gametophytic tissue grew up around the proembryo to imbed it.

The condition shown in the hibernal embryo of figure 17 was found several times. Figure 18 shows one of several hibernal embryos in which only one small cell near the lower end contained dense cytoplasm, and in which most of the prosuspensor cells in the tiers above were short, as if their elongation had included two tiers of cells, now slightly displaced. All of the hibernal embryos referred to above were deeply imbedded within the tip of the female gametophyte, but that shown in figure 19, situated much nearer to the surface, presents an unusual arrangement of cells in an hibernal stage which includes only five or six cells. Its elongated shape seems to indicate that it has suffered considerable distortion during its envelopment by the margin of the female gametophyte. It did not become as deeply imbedded
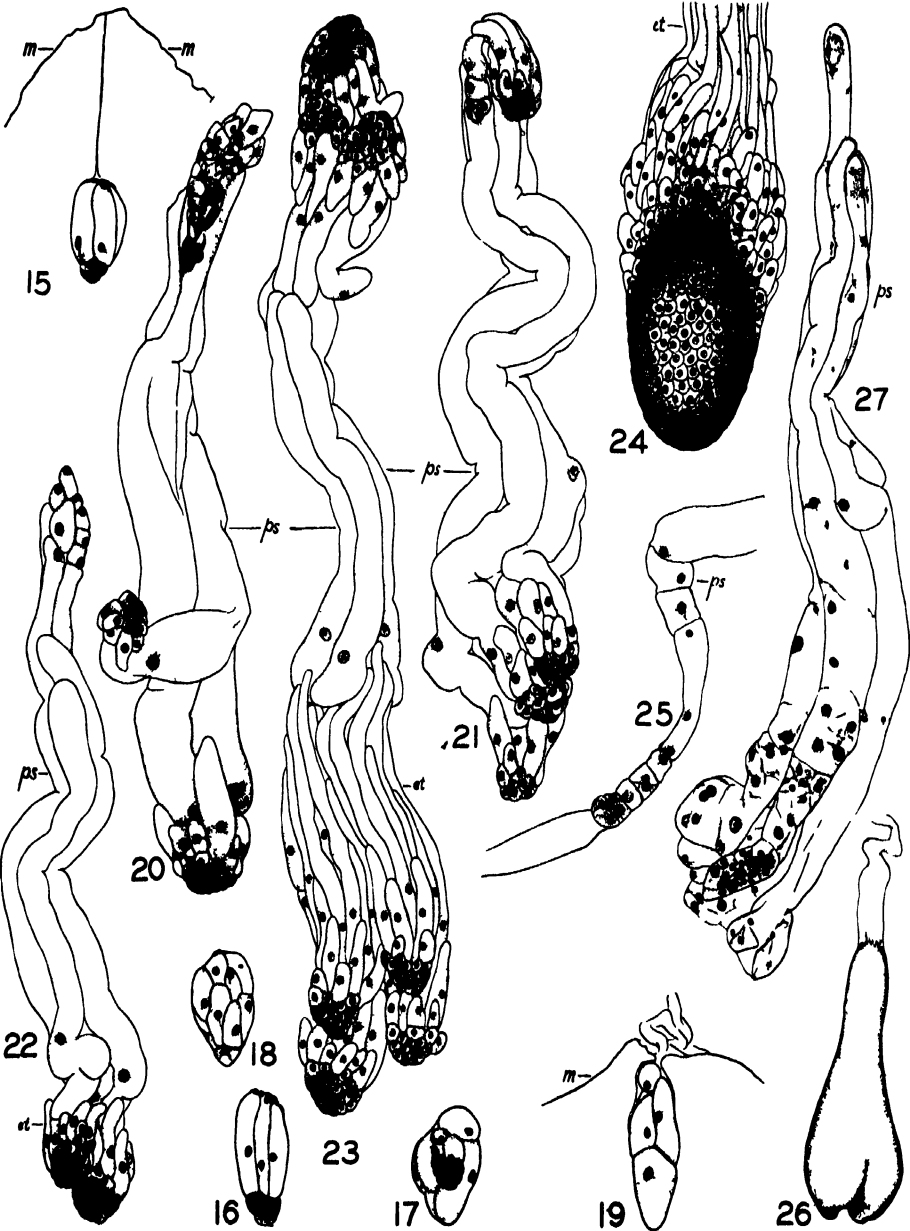
as usual and the remains of the pollen tube may be seen crushed against the top. Figure 19 is, no doubt, abnormal but it is reproduced because it indicates that the hibernal embryos may owe the variability in their internal cell-orientations and arrangements to accidental displacements suffered during the period when the gametophyte envelops the proembryo. Such arrangements as are found in figures 17 and 18 may be due, at least in part, to this cause. It seems probable that the embryo of figure 19 would, should it resume growth, push out and downward on the side facing the observer. Many of the irregularities observed in later stages may be attributed to variations in cell number and arrangement in the hibernal embryo.

In the proembryo stages of September and October collections, 3 of 28 ovules with proembryos were found in which two eggs had been fertilized. Figure 13 shows a pair of proembryos resulting from the fertilization of neighboring archegonia. To sum up, while usually only a single archegonium is fertilized, plural fertilizations were observed in about 10 per cent of the ovules. However, I have not recognized such pairs of hibernal embryos in about 18 ovules that were beginning to enlarge in the spring. These should be easily recognized by dissection.

The next stage obtained was from ovules which had grown to full size. These embryos are shown in figures 20–22. In each of these we find several multicellular embryos, already beginning to form massive secondary suspensors, attached to the lower end of the fully elongated prosuspensor composed of 4 or 5 cells. One of these, probably the largest terminal embryo, is destined to become the dominant embryo which survives in the matured seed, where almost invariably only a single embryo remains. Above the prosuspensor a group of cells is usually found which are in the position of rosette embryos. However, an examination of the series of arrested proembryos indicates that there is usually no rosette tier. They may have come from the subdivision of some of the cells of the hibernal embryo which did not elon-

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Explanation of figures 15–27

FIGS. 15–26. *T. nucifera*. FIGS. 15–19. Hibernal embryos. × 55. FIGS. 15–16. As found imbedded near tip of female gametophyte near micropyle with margin of endosperm shown at *m*. FIG. 17. Proembryo with cell arrangement disturbed so that embryonic cells are beside prosuspensor cells. FIG. 18. Proembryo with larger number of cells. FIG. 19. Proembryo abnormal owing to disturbance caused by overgrowth of female gametophyte. FIGS. 20–22. Early embryo with prosuspensors elongated (from full grown ovule). × 45. FIG. 23. Slightly older embryo system after terminal embryos have developed massive secondary suspensors and several embryos have developed in region above prosuspensor. × 45. It is possible that these upper embryos belong in the same position as those in figure 21, and were disturbed in dissection and mounting. FIG. 24. Largest embryo obtained before cotyledons have appeared. × 55. FIG. 25. A single prosuspensor cell from an older embryo system which has given rise to embryonic masses. × 55. FIG. 26. Mature embryo dissected from seed. × 18. FIG. 27. Isolated prosuspensor of *T. californica* showing embryos developing from cells of prosuspensor, at first by free nuclear division followed by wall formation and ordinary cell division.

gate in the uppermost tiers of the prosuspensor, situated in such hibernal embryos as those shown in figures 17 and 18. In figure 21 a pair of small embryos is shown in the position of rosette cells. Figure 23 shows three embryos in this position apparently growing in the direction of the micropyle. However, one cannot be certain that these embryos were actually oriented in this inverted position within the gametophyte before dissection. It is entirely possible that embryos in the position above the prosuspensor shown in figure 21 may have become folded upward during dissection or subsequently during staining and mounting to give the appearance of figure 23. None of the embryos appears to have apical initial cells.

The prosuspensor cells in all of these figures (figs. 20–23) are uninucleate. In an older embryo system of which figure 24 represents the largest terminal embryo, some of the prosuspensor cells have several nuclei. Possibly some of these prosuspensor cells are beginning to form internal embryonic masses. Figure 25 shows an abnormally developed embryonic mass of cells found among the prosuspensor cells of another embryo system, which may have been derived from the subdivision of a prosuspensor cell. However, its diameter is much less than the usual size found in these cells. This is mentioned because of the peculiar behavior of the prosuspensor cells usually observed in *T. californica*, which is not shown, save for a few exceptions, in this species.

The embryogeny of *T. nucifera* includes no primary suspensor. Immediately below the prosuspensor a massive secondary suspensor is found, which is formed from the elongation of cells situated in the proximal region of the embryo. The terminal embryo shown in figure 24 has formed a massive secondary suspensor and is becoming cylindrical, but is still without internal organization of tissues. Soon after this stage the plerome of the root tip, the stem tip, and cotyledons would be expected to become organized. I obtained no embryos in this stage, but figure 26 shows (on a scale of magnification one-third that of figure 24) the mature embryo with its cotyledons, as it was removed from a ripe seed of *T. nucifera*. Its cotyledons are very short and have a retuse or slightly indented tip. The embryo occupies only a relatively small space, restricted to the axis of the upper fifth of the endosperm. When compared with the embryos of other conifers the embryo of this species is still relatively immature when the seed is ripe; it must still undergo considerable development within the seed after planting, before any part of it is ready to emerge from the seed coats. Several dozen were dissected from seeds and they were almost all of the same size and stage of development as in figure 26.

The endosperm or matured gametophytic tissue shows a distinct irregularity in its outer surface, due to the rumination of the female gametophyte. Rumination is less extensive than in other species. The sinuses shown in a cross section of the seed are not so deep or so numerous as those of *T. cali-*

fornica or *T. taxifolia.* There are usually three principal sinuses which extend less than half way inward from the margins to the centre and there are many minor corrugations.

Torreya californica. In this species the hibernal embryos were not observed. Miss Robertson has shown the initial steps in the organization of the proembryo. Three of her proembryo stages are somewhat diagrammatically reproduced in figures 28–30, redrawn at the same scale of magnification as my figures of dissected embryos. They are from very early stages, soon after fertilization, and before the gametophyte has enveloped them. There is little doubt that these proembryos will still undergo enlargement before they become dormant or inactive, and should not be considered the equivalents of the hibernal embryos of figures 15–18, as found in *T. nucifera* in the subsequent season.

According to Miss Robertson's account of the proembryo, the two nuclei resulting from the first division of the zygotic nucleus are found in the lower part of the archegonium. Another nuclear division follows before any walls are formed. The upper nuclei, still incompletely walled off from the upper cytoplasm of the egg (figure 28), undergo additional divisions, which result in a proembryo with several tiers of cells. Figure 29 shows this stage, which has a terminal cell below, above this a tier of two or three cells, and four or five cells forming the prosuspensor tier. Above these are several relict nuclei which soon disintegrate. Following one or two other investigators of this period Miss Robertson labeled these upper nuclei the rosette, but the latter term should be applied to walled cells, above the prosuspensor, which fail to elongate. The prosuspensor tier elongates until it fills the archegonium completely, crushing the remains of the relict nuclei above them (figure 30).

While the proembryo of *T. californica* has not been observed in later stages or in the hibernal stage in the subsequent season, it may be presumed to enlarge considerably from the size shown in figure 30. The hibernal embryos shown for *T. nucifera* and those of *T. taxifolia* must for the present serve to supply this gap in the embryogeny of *T. californica*, with an allowance for size, since the archegonia of the latter are larger at the time of fertilization.

There is also the possibility that, at least occasionally, there may be two or more hibernal embryos in *T. californica*, resulting from the fertilization of eggs in separate archegonia. Of course, plural fertilizations would depend also upon the presence of more than one pollen tube, since the archegonia are separated so that only one egg may be fertilized by a pollen tube. For these reasons it is not certain that more than a single hibernal embryo would be found in *T. californica* except in well-pollinated material.

Figure 32 represents an embryo system of *T. californica*, in a stage comparable to the older stages shown for *T. nucifera*. There are four prosus-

pensor cells, bearing five embryos below on massive secondary suspensors, and a smaller embryo in which the secondary suspensor has not developed. As in *T. nucifera* there is no primary suspensor, and no apical initial cell. The nuclei in the elongated cells of the prosuspensor have divided a number of times, and cell walls are beginning to form as the ends of these prosuspensor cells are becoming embryonic.
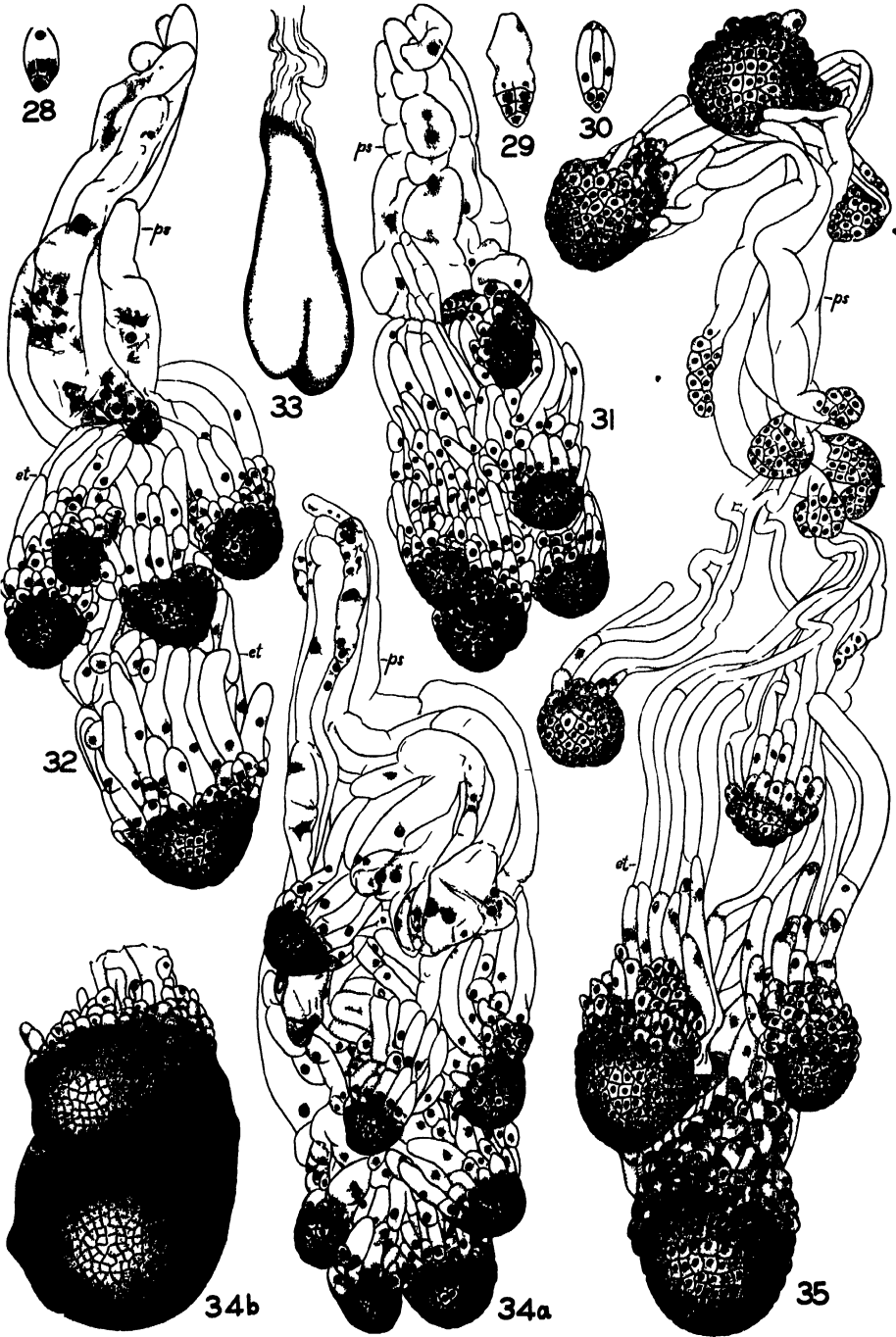
Figure 27 shows a prosuspensor of *T. californica* which has been isolated from a system and which shows how its cells give rise to embryos after they have become elongated. The first steps are free nuclear divisions, followed by wall formation after a considerable number of separate nuclei have been formed; then cell plates begin to appear after each nuclear division. The embryos formed by this manner of budding from prosuspensor cells are often very misshapen and abnormal in appearance.

Figure 34a shows a similar embryo system which is considerably older. Six or seven prosuspensor cells and also a larger number of embryos are found. The largest embryo, on the end in this system, was broken off in dissection and is shown separately in figure 34b. It is two-lobed, a feature which may be only a later development of an embryo similar to the terminal one shown in figure 31. It was found difficult to dissect out the entire embryo system intact when the largest terminal embryo was of the size shown in figure 34b. These oldest embryos were firmly imbedded in the endosperm and could be obtained only by removing the gametophytic tissue around them a little at a time. Figure 35 shows the largest embryo system of *T. californica* which was successfully removed. Here the prosuspensor cells have all formed embryos from their lower ends by a process of budding, and well developed secondary suspensors have been formed in the larger embryos. There are a few embryos situated above the prosuspensor which may have developed from the upper end of some of the prosuspensor cells as shown in figure 34a, where one of the cells of its prosuspensor is in an early stage of budding above.

It is also possible that figure 35 may represent the embryos of more than one zygote, on the supposition that two archegonia were fertilized (by separate pollen tubes) and became closely associated as hibernal embryos. In this figure the prosuspensors do not show the upper origin clearly.

Figure 32 has four elongated cells in its prosuspensor, but in figure 34a there are at least six or seven. Miss Robertson places the number of such cells

in the proembryo immediately after fertilization at five or six, but it is possible that their number may sometimes be increased or decreased by rearrangement of cells or by an abortion of cells in the hibernal embryo.

From living ovules no embryo was obtained larger than that showing in figure 34*b*. In this embryo primordia of the cotyledons had not been formed. Two cotyledons were found in the seeds of this species, and they are probably formed as in the other species, except that the embryo is larger in all comparable stages. Figure 33 shows an embryo dissected from a matured seed of the species at one-third the magnification used in the other illustrations. This embryo has a different form from that of *T. nucifera*, has longer cotyledons whose ends are rounded and are unequal in length. The entire embryo is somewhat larger. However, even this embryo is still very immature in a fully matured seed when compared to other genera of Taxads and to other conifers.

The general impression gained from the previous accounts, which were very largely confined to the proembryo, was that simple polyembryony prevails. The surprising feature in the embryogeny of the Torreyas is the nature and extent of their cleavage polyembryony. It appears that each zygote may produce at least as many embryos as there are cells in the early proembryo, sometimes as many as there are cells in the hibernal embryo. Even the prosuspensor cells of *T. californica* add more embryos to the large number which would have their origin from the cells of the lower tier or tiers of a proembryo.

The endosperm is more extremely ruminated in this species than in *T. nucifera*. The sinuses are more numerous and extend more than half way to the center of the endosperm.

Torreya taxifolia. Coulter and Land have given a detailed account of the development of the gametophytes, fertilization, and proembryo of *T. taxifolia.*

The mean dimensions of 7 female gametophytes of *T. taxifolia* before fertilization were found to be 173×270 μ. These dimensions are somewhat less than those given by Coulter and Land (200×300 μ). Their account must be modified only as explained in an earlier part of this description, since the cytoplasm of the male cells is abandoned and is not contributed to the zygote. The single archegonium of *T. taxifolia* would not be so much smaller than that of *T. californica* if it were still all present and fully recognizable at the time of fertilization. For the same reason the proembryo of *T. taxifolia* may fill the egg completely even before much elongation of the prosuspensor cells has taken place, and the latter may enlarge very little before the archegonium is completely filled. However, the prosuspensor cells do elongate and enlarge slightly during the period of enlargement of the female
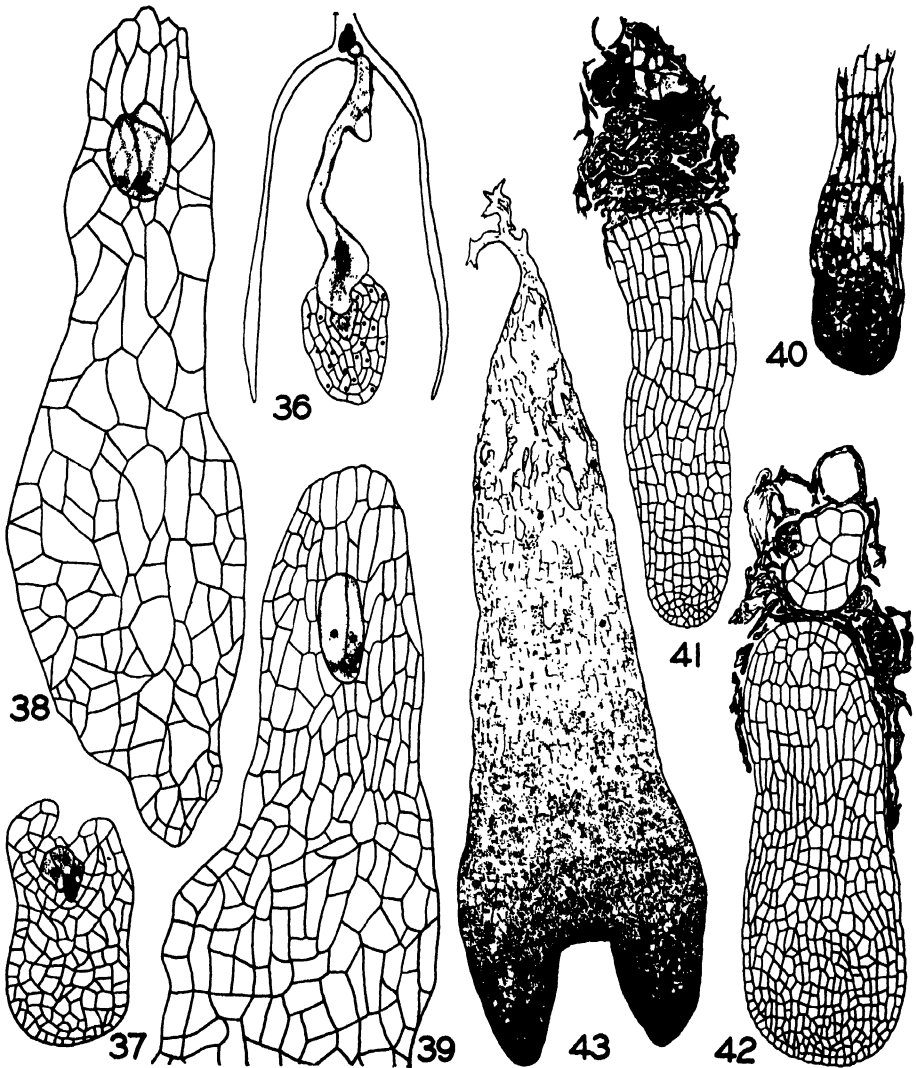
FIGS. 36–43. *Torreya taxifolia.* FIG. 36. Relation of gametophytes in nucellus before fertilization. × 60. FIG. 37. Female gametophyte with proembryo being enveloped and passing into hibernal embryo. × 60. FIG. 38. Hibernal embryo in spring after beginning of enlargement of ovule. × 60. FIG. 39. Hibernal embryo in later stage showing upper half of endosperm. × 60. FIGS. 40–42. Sections of embryo on secondary suspensor with remains of smaller embryos resulting from cleavage polyembryony. FIG. 43. Section of mature embryo of seed. × 60.

gametophyte, as may be seen in the series of figures 36–39. This series of draw-
ings serves to emphasize the small size of the gametophyte at the time
of fertilization and shows the changes which take place in the gametophyte
and embryo after fertilization. Figure 36 is a drawing reconstructed from
four adjacent sections, showing the nucellus before fertilization, with the
cavity occupied by the pollen tube after the latter has made contact with the
archegonium. The pollen tube shows a body cell which is still undivided, and
below it the stalk and tube nuclei. Figure 37 shows a stage of the game-
tophyte some time after fertilization, with a small proembryo completely fill-
ing the archegonium and becoming imbedded within the tip of the female
gametophyte, which has enlarged slightly. Figure 38 shows a female game-
tophyte in the subsequent spring which has enlarged considerably, with the
hibernal embryo completely imbedded. The female gametophyte shown in
figure 39 has enlarged so much that only the upper half of it is shown. It has
enlarged to a length of 2.5 mm. and is 5 or 6 times as long as that of figure 37.
However, it is still to undergo a 10-fold enlargement in length before its full
size is attained. Figures 37–39 show the relative inactivity of the hibernal
embryo during this period of rapid growth of the female gametophyte, which
may now be spoken of as endosperm. Coulter and Land state that the embryo
during this period may consist of 12–18 cells. It is possible that some of the
embryos (figures 37–39) do not have this number of cells, nor are they all
organized in three tiers. However, the variations observed in the hibernal
embryos of *T. nucifera* (figures 15–19) indicate that any differences in 2-
tiered or 3-tiered organization may be of minor importance. As shown above,
the corresponding stages in the hibernal embryos of *T. nucifera* and *T. taxi-
folia* pass through similar stages and, no doubt, those of *T. californica* do
likewise, though they may be somewhat larger.

The stages which follow the elongation of the prosuspensor in *T. taxifolia*
are probably very similar to figures 21 and 22 of *T. nucifera*. Figure 40 shows
the cellular details of an embryo with the lower part of the secondary sus-
pensor before the differentiation of the meristems that give rise to the root
tip, cotyledons, etc. Figures 41 and 42 show later stages in which the remains
of smaller embryos may be seen. They have been pushed upward by the
rapidly elongating massive secondary suspensor.

Coulter and Land (5) mentioned the occurrence of secondary embryos
observed in the second season, in the region above the secondary suspensor
of the well enlarged embryo. No doubt they observed the conditions shown in
figures 41 and 42. However, their suggestion that some of these may have had
their origin in some kind of apogamy is superfluous in the light of the facts
concerning the prevalence of cleavage polyembryony in the Torreyas.

Figure 43 shows a section of a mature embryo with its two cotyledons.
This embryo is smaller than that of the other two species, since this figure

was drawn to the same scale as those of the younger embryos. These figures make it clear that cleavage polyembryony is also found in *T. taxifolia,* though it may be less extensive. Cleavage polyembryony is not as easily demonstrated from sections as from dissected preparations.

The endosperm is ruminated with deep sinuses and many other grooves and corrugations comparable to those of *T. california.*

Austrotaxus spicata Compton. Figure 44 shows an embryo complex from the fertilization of 3 archegonia in *Austrotaxus.* This was dissected in 1927 from one of several ovules obtained from herbarium collections. This ovule had been preserved in formalin and came from one of Compton's original collections. The slide was left on deposit at the Arnold Arboretum. Unfortunately, the largest embryo was so firmly imbedded that it was broken off and not recovered, as shown by the broken ends of the prosuspensor.

By itself this single stage had little value. The writer had hoped to obtain additional material in earlier and later stages from which at least a partial account of the embryogeny might be given. In the meantime Saxton (15) has obtained sufficient material for a study of the morphology and proembryo. Figure 44 may, therefore, be included here because it adds a later stage to Saxton's account.

The striking feature shown by this figure is the very long prosuspensor. It also confirms the absence of cleavage polyembryony, as reported by Saxton, and the absence of a cap in the early embryo. The larger size and pointed shape of the archegonia shown by Saxton's figures, as well as the extent of elongation of the prosuspensor shown here, stand out in contrast with the small size of the archegonia and the relatively shorter prosuspensor found in *Taxus* (7, 8, 10). The only differences found between figure 44 and the oldest embryo illustrated by Saxton are the much longer prosuspensor and the absence of a rosette in each of the three embryos shown. Saxton found a rosette present at a much earlier stage of the embryo. It is not likely that I overlooked the remains of a rosette group which may have been present at an earlier stage, since I searched for these embryonic features with special care. The rosette is variable in its occurrence in some other conifers, notably in *Podocarpus spicatus.* A few scattered rosette cells have been observed in *Taxus* (8), but are found very rarely. The rosette is also variable in its occurrence in *Sciadopitys* and elsewhere. The difference between Saxton's record and my figure of the embryo is, therefore, not important except as it may indicate a similar variability in *Austrotaxus.*

At the time when the embryo of figure 44 was dissected out, I was especially interested in the possible occurrence of binucleate cells in the early embryo of conifers. Binucleate cells have been found in the early embryos of fourteen species of Podocarpaceae and only in the embryos of mem-
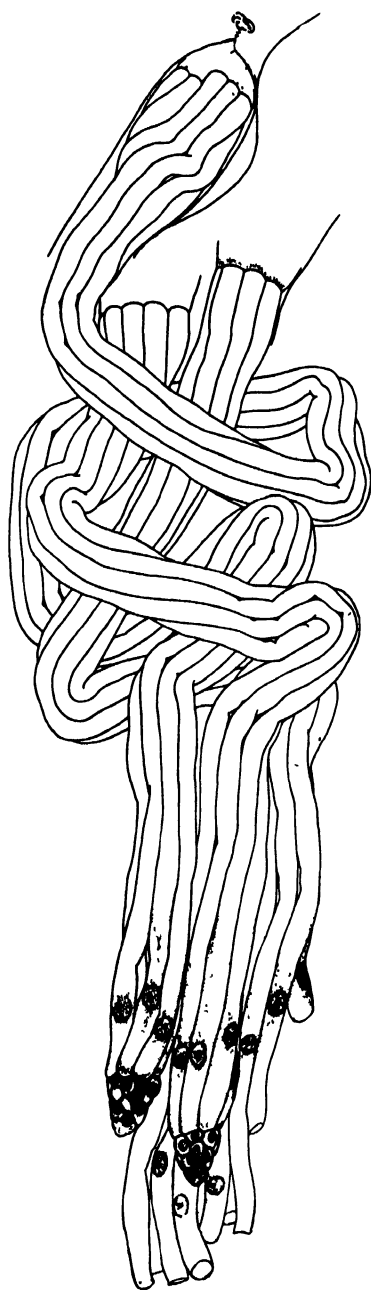
FIG. 44. Embryo system from an ovule of *Austrotaxus spicata*. From collection of Arnold Arboretum. × 90.

bers of this family. This includes *Saxegothaea conspicua*, investigated very recently by Doyle (6). While figure 44 does not show binucleate cells, I concluded at the time that these embryos may be past the stage when they would be binucleate. It is, therefore, significant that Saxton did not observe a binucleate condition in his earlier stages, nor has anyone found this condition in genera belonging to families outside of the true Podocarpaceae. Saxton's investigation has shown the absence of the terminal cap cell or group of cells at the end of the proembryo and early embryo; this is likewise indicated by my figure. The deciduous cap of the embryo was first observed by Strasburger in *Cephalotaxus Fortunei* (18), and has been confirmed by more recent investigators. The embryo of *Amentotaxus* has not been investigated; Saxton indicates that it bears a close resemblance to *Cephalotaxus*.

Saxton, who reviewed the comparative morphology of this group, concluded that *Austrotaxus* is a form which stands in a position intermediate between *Taxus* and a prototype which may be common to *Cephalotaxus* and *Amentotaxus*, as well as to the Torreyas. All of the new embryological facts brought out by my investigation are in general agreement with Saxton's scheme of phylogeny.

DISCUSSION

Fertilization. The process of fertilization undoubtedly merits additional investigation in conifers. The record has stood for many years that cytoplasm of the male cell contributes to the fertilized egg in *Torreya*, but I have found the evidence to the contrary. Land (9) made the statement in his study of *Thuja occidentalis* that only the nucleus enters into the zygote, and several of his figures show the abandoned cytoplasm at the neck of the archegonium. However, a few years later Coulter and Land (5) described fertilization in *Torreya taxifolia* as including male cytoplasm. Miss Robertson (13) had pointed out and Coulter and Land also showed a sheath of denser cytoplasm surrounding the fusion nucleus. The presence of this cytoplasmic sheath in *Torreya* seems to be the only evidence offered for the inclusion of male cytoplasm.

That this distinct cytoplasmic sheath may have a different origin is indicated by the fact that it is already beginning to appear before the egg is fertilized (see figure 14). It is shown in Coulter and Land's figure 23, plate II, also, less distinctly, in Miss Robertson's figure 14, plate 8, both of unfertilized eggs. Even if this zone becomes more pronounced after fertilization it is unnecessary to assume that it had its origin in a contribution of male cytoplasm.

None of the previous investigators of *Torreya* mentioned the abandoned cytoplasm of the male cells which is left behind. However, it is shown at the right of the neck of the archegonium in Coulter and Land's figure 24, which shows that a naked male nucleus below is crossing the dense zone of cytoplasm

in fertilization. Miss Robertson (13) shows the abandoned mass of male cytoplasm in figures 19, 23, and 24 of plates 8 and 9, where it is the largest of the objects labeled *n.c.* This abandoned cytoplasm is devoid of a nucleus but sometimes contains chromidial bodies.

Sinnott (17) shows a very distinct zone of deeply-staining cytoplasm surrounding the egg nucleus before fertilization, as well as after fusion of the sexual nuclei, in *Podocarpus ferrugineus* and *Dacrydium Bidwillii* in his plate V, figures 2 and 3. His photomicrographs, figures 34 and 41, show this for *P. dacrydioides*, before fertilization. In his figure 35 the sheath of dense cytoplasm is present on all sides of the egg nucleus before the male nucleus has made contact. Furthermore in figures 36 and 42, showing the first division of the sporophyte, this zone is less distinct than before fertilization; in figure 42 this zone is destroyed on the upper side where the male nucleus passed through it, where it would be expected to be most abundant if actually contributed by the male cell.

I feel convinced from my own investigations of *Torreya* that the dense zone of cytoplasm surrounding the fusion nucleus before and after fertilization is not the male cytoplasm, and that the male nucleus which fuses with the egg nucleus is shed from the cytoplasm of the body cells. Only a negligible trace of male cytoplasm from any source is likely to enter into that region of the egg which is likely to be included in the embryonic cells of the proembryo.

A new feature which was observed indicates that in Torreyas the male cells do not become separated from each other. The two male nuclei emerge at different places in the common cytoplasm of the double male cell.

Phylogeny. There is little doubt about the fact that *Torreya* is a highly specialized genus of the Coniferae. All species of *Torreya* have wingless pollen grains without prothallial cells, have unequal male nuclei in their pollen tubes, and none of the features associated with the more primitive conifers. The absence of a megaspore membrane, the fact that walls appear in the proembryo after 4 free nuclei have formed, the small archegonia with absence of an archegonial jacket, the specialized condition of an hibernal stage in the embryo associated with the prolongation of the embryogeny into two seasons, dicotyledonous embryos, and the ruminating endosperm are all advanced features. The ovule is at maturity the largest and most specialized of those of all the conifers.

Torreya nucifera shares with *T. californica* all the primitive features of the gametophytes and embryo. Like the other vegetative and reproductive structures, the female gametophytes may be larger in the latter species; the archegonia also are considerably larger, differing in about the same ratio or possibly more. Otherwise, however, in the number of archegonia, in the

number of their neck cells, in the general character of the proembryo, which occupies only the lower portion of the egg, these two species are in very close agreement. It is also possible that the occasional plurality of hibernal embryos resulting from the fertilization of two archegonia in *T. nucifera* may be duplicated in *T. californica,* in well pollinated material. This feature cannot be duplicated in *T. taxifolia,* in which there is usually only a single archegonium.

The three species agree further in having walls appear in the proembryo after the four nuclei have been formed, a condition which seems to be unaffected by variations in the size and shape of the archegonia. The three species have similar conditions of cleavage polyembryony, with a number of embryos resulting from various cells in the hibernal embryo. However, *T. californica* adds to the polyembryony through budding, resulting from extensive subdivision of the tips of the prosuspensor cells. It appears that all three species may have embryos in the position of rosette embryos, and there is no essential difference, save that of size, in the matured embryos of the seeds. They are all dicotyledonous, with the possibility of inequality of length in cotyledons of *T. californica.*

With respect to the rumination of the endosperm both *T. californica* and *T. taxifolia* are much more advanced than *T. nucifera.* I have examined a considerable number of the latter but only a few of *T. californica.* Coulter and Land (5) have given an excellent photographic reproduction showing the shape and the extent of the rumination of *T. taxifolia. T. nucifera* shows the least complexity; the endosperm is described by Pilger (11) as folded or pleated and corrugated. The seeds which I examined had the three deepest longitudinal sinuses extending to less than half the distance to the center, and there were many smaller wrinkles and corrugations between them. *T. Fargesii,* which was not available for study, is described by Pilger as having its endosperm ruminated half way to the middle. The endosperm of *T. californica* and *T. taxifolia* has sinuses extending more than half way to the middle of the ovule. This agrees in general with the order given in Pilger's monograph, which treats *T. nucifera* first as the more primitive species, but it appears from the present study that *T. taxifolia* is the most specialized.

The advanced morphological features in the Torreyas are all found in *T. taxifolia.* In this species the pollen tube arrives relatively sooner and remains so long in contact with the archegonium that it not only destroys the pair of neck cells, but also shortens the archegonium, to give the appearance later of a proembryo which fills the entire archegonial cavity at the time of wall formation. These features, as well as the extreme reduction in the number of archegonia to one (very rarely two) marks this species as the most advanced. In general, therefore, the three species stand in the following phylogenetic order: *T. nucifera, T. californica, T. taxifolia.*

Saxton (16) in his study of the morphology of *Austrotaxus spicata*, points out the probable phylogeny of the Taxaceae, consisting of 5 genera which include *Torreya*. He considers three groups or branches derived from the same prototype and places *Torreya* by itself at the end of one branch, *Cephalotaxus* above *Amentotaxus* at the end of another, and *Taxus* at the end of another branch, with *Austrotaxus* as a more primitive form or connecting link.

It is only in following such an arrangement that the writer can relate to each other the groups included in the taxad genera. They have diverse embryogenies when compared. In *Taxus* and *Austrotaxus* simple polyembryony prevails, in *Cephalotaxus* we find simple polyembryony for the main terminal embryo, which is borne on the end of a prosuspensor and is terminated by a deciduous cap, but we have a form of cleavage polyembryony (determinate in character) since the rosette cells give rise to small embryos. None of the groups has the deciduous cap in the early embryo except *Cephalotaxus*. Thus, one group represented by *Torreya* has retained cleavage polyembryony while both of the other two groups have lost it. One of them shows distinct evidence of having been derived from a prototype with cleavage polyembryony, while the other shows the evidence for such a history less distinctly, but the embryonic cells still possess the potentialities.

In support of the latter statement we need only to refer to Jäger's (8) observations on *Taxus*, which the writer has verified in part. Jäger states that the suspensor cells which do not elongate fully but become separated from the rest (of the prosuspensor) undergo nuclear divisions, and form embryos within these cells. He illustrates several misshapen embryos of this kind in plate XIX, figures 75a, 75b, 75c and 75d. As he states, not only the terminal group of cells which actually contribute the embryo are embryonic, but also the cells of the upper tier strive to form embryos, which become aborted soon after they form a tissue of several cells. This also marks the group of elongating cells in *Taxus* as constituting a prosuspensor, and these potentialities support the view that cleavage polyembryony may have been present in the history of *Taxus*, although it is the genus in which it is now most completely eliminated. Of course, Saxton's phylogenetic arrangement, which I am accepting, is supported by many other morphological facts.

SUMMARY

1. *Torreya nucifera* is similar to *T. californica* in having from two to four (usually three) archegonia. *T. taxifolia* usually has only one archegonium.

2. None of the species of *Torreya* forms the ventral canal nucleus.

3. The megaspore membrane is absent in all species, or so thin that it is not usually observed.

4. The female gametophyte is smallest in *T. taxifolia,* somewhat intermediate in size in *T. nucifera,* and is largest in *T. californica,* at the time of fertilization.

5. The pollen tube in *T. taxifolia* reaches the female gametophyte very early, sometimes before cell walls are formed, and is in intimate contact with the archegonium throughout its development, invading and digesting the neck cells and the upper portion of the archegonium. In *T. nucifera* the neck cells persist and vary in number from two to eight. The usual number is four.

6. At fertilization the male nuclei are released from the cytoplasm surrounding them in the double male cells, which do not become separated. This abandoned cytoplasm is usually found in the upper portion of the egg, where it does not contribute to the cytoplasm included in the zygote.

7. The proembryo of all three species of *Torreya* forms four free nuclei before walls appear and, with the exception of that of *T. taxifolia,* the proembryo occupies only a portion (about two-thirds) of the space in the archegonium; in the latter species, where a part of the archegonium is destroyed, it may occupy all of the space that remains.

8. The proembryo passes into an 8-celled stage; from this into a proembryo of 12–16 cells, in which the tiers are not equal in the number of their cells and the cells not always arranged in distinct tiers. This is followed by a slight elongation of the prosuspensor cells in the uppermost tier, followed by an inactive period to form the hibernal embryo.

9. In *T. nucifera* more than one archegonium may sometimes be fertilized, giving rise to two embryo systems. In *T. taxifolia,* which has only a single archegonium, only one embryo system is possible.

10. Cleavage polyembryony is a constant feature in *Torreya.* In the season following fertilization the hibernal embryo forms a system of several embryos borne on the end of a prosuspensor of from three to five or more elongated cells.

11. Embryos may arise in the rosette region, but the exact manner of origin of rosette embryos remains uncertain and may be variable.

12. In *T. californica* the prosuspensor cells may become multicellular by division of their nuclei and give rise to additional embryos through a form of budding in the second season. In *T. nucifera* budding from the prosuspensor cells was not usually found.

13. The mature embryo of the seed has two cotyledons in all three species. In *T. californica* the cotyledons were found to be unequal in length.

14. The female gametophyte forms the endosperm, which is only slightly ruminated in *T. nucifera,* and becomes very deeply ruminated in *T. californica* and *T. taxifolia.*

15. *Torreya* occupies a very high position in the phylogeny of conifers.

The species of *Torreya* may be arranged in the following order of complexity:
T. nucifera, *T. californica*, and *T. taxifolia*.

16. The phylogeny of Taxaceae suggested by Saxton has been confirmed.

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MACROSPOROGENESIS AND THE DEVELOPMENT OF THE EMBRYO SAC IN YUCCA ALOIFOLIA

FRED T. WOLF

(WITH FIFTEEN FIGURES)

The development of the macrogametophyte or embryo sac in the Angiosperms has now been worked out in a considerable number of genera and species. Although no fewer than ten types of embryo sac development, involving variations in the number of functional macrospore nuclei and the number of nuclei in the mature embryo sac, are described in a recent review of this subject by Maheshwari (1937), perhaps 95 per cent of all the forms which have been studied are characterized by a "normal" development, involving the formation of an 8-nucleate embryo sac from a single functional macrospore.

The formation of the macrospores and the subsequent development of the macrogametophyte in the genus *Yucca* (Liliaceae, tribe Dracaenoideae or Yucceae) have been studied by a number of investigators. The hypodermal position of the archesporial cell and its division to form an outer parietal cell and an inner macrospore mother cell were observed by Vesque (1879), Guignard (1882), and Hérail (1889). Working with the same species, *Y. gloriosa,* all three of these investigators were led to believe that the division of the macrospore mother cell resulted in the formation of only three macrospores. The presence of an axial row of four macrospores in this genus was apparently first noted by Koernicke (1901) in *Y. filamentosa,* and has been confirmed by subsequent investigators.

Fairly complete accounts of the development of the embryo sac have been given for *Y. gloriosa* by Guignard (1882), for *Y. filamentosa* by Reed (1903), for *Y. glauca* by Folsom (1916), and for *Y. rupicola* by Watkins (1937). All species of the genus hitherto investigated have been shown to have an embryo sac of the "normal" type, the accounts of the various investigators differing only in the arrangement of the macrospores in the tetrad and the identity of the functional macrospore.

The chromosomes of *Y. aloifolia* root tips have been studied by Müller (1910), who found that the diploid complement included 54–56 small chromosomes plus 10 large ones. More recently McKelvey and Sax (1933), in a number of species of the genus, report $n = 30$, consisting of 5 large and 25 small chromosomes.

MATERIALS AND METHODS

The species which forms the basis of the present report is *Yucca aloifolia* L., which is described and illustrated in the monograph of Trelease (1902).

Flower buds of various sizes were collected in July 1938 from plants grow-
ing near the Duke University Marine Laboratory, on Piver's Island, near
Beaufort, North Carolina. Securing the desired variety of developmental
stages was greatly facilitated by the fact that the inflorescences contain
flowers of different ages, a given stalk bearing very young buds at the apex
and at the same time mature flowers ready for pollination near its base.
The pistils were removed from the buds, the larger ones being sliced into
several pieces to insure thorough penetration of the fixative, and fixation
was carried out using Karpechenko's modification of Navashin's solution.
After washing, the material was dehydrated and cleared in an ethyl alcohol-
butyl alcohol series, and imbedded in paraffin. Transverse sections of the
pistil were cut at a thickness of 10 μ, and the sections were stained with
Heidenhain's iron alum hematoxylin.

OBSERVATIONS

The ovary in *Y. aloifolia*, like that in other members of the genus, is
superior, and consists of three fused carpels. Placentation is axile, and
cross sections of the ovary show that the anatropous ovules are borne in six
rows, two in each locule.

The youngest ovules examined show, near the micropylar end of the
nucellus, a macrospore mother cell and an outer parietal cell (fig. 1), result-
ing from the prior division of an archesporial cell which is hypodermal in
position. The large nucleus of the macrospore mother cell contains a single
nucleolus and conspicuous chromatic strands during the prophases of the
heterotypic division. Chromosomes are differentiated and become aggre-
gated on the equatorial plate (fig. 2). Following the completion of the
heterotypic division, a cell wall is formed, separating the two component
cells of the dyad (fig. 3). A metaphase stage of the succeeding homoeotypic
division is shown in figure 4.

The meiotic divisions result in the formation of a tetrad of macrospores
(fig. 5), which usually, although not always, show a "T-shaped" arrange-
ment with the micropylar pair lying side by side. An axial row of four
macrospores in a linear arrangement has been observed, but apparently this
is of much less common occurrence, the "T-arrangement" being the rule.

Explanation of figures 1-7

FIG. 1. Macrospore mother cell and parietal cell. × 480.

FIG. 2. Equatorial plate stage of heterotypic division. × 480.

FIG. 3. Two cells resulting from heterotypic division. × 360.

FIG. 4. Equatorial plate stage of homoeotypic division. × 360.

FIG. 5. Tetrad of macrospores in "T-arrangement." × 360.

FIG. 6. Developing chalazal macrospore, with remnants of two disintegrating macro-
spores; two tapetal cells. × 480.

FIG. 7. Developing chalazal macrospore, with remnants of two disintegrating macro-
spores. × 480.
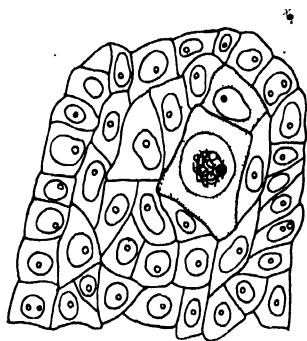
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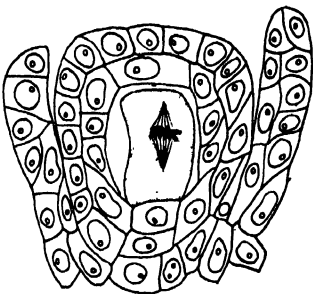
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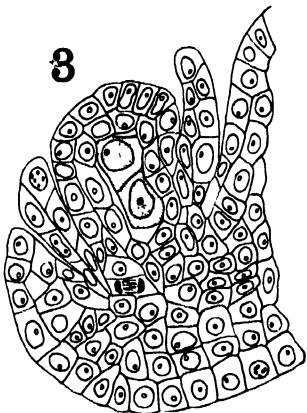
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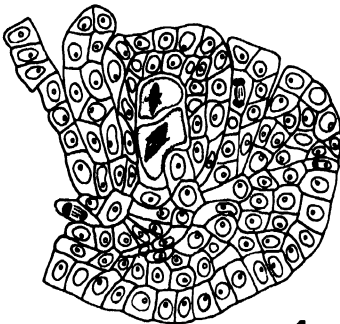
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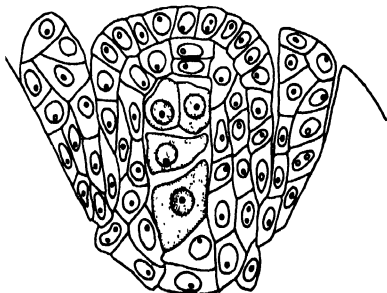
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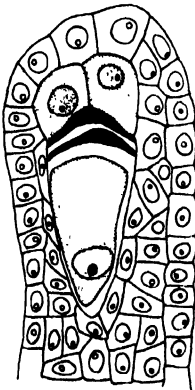
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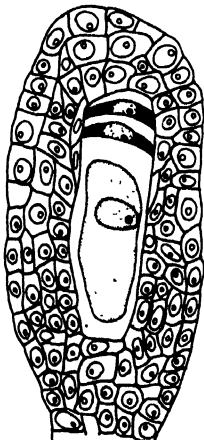
7

The parietal cell, differentiated by division of the archesporial cell, divides during macrosporogenesis to form two tapetal cells (fig. 6), whose contents are soon to be utilized in the development of the macrogametophyte. In all cases observed with certainty, it is the chalazal macrospore which develops into the embryo sac.

As the chalazal macrospore enlarges, the three remaining macrospores are crushed, and their deeply-staining remnants persist for a short time (figs. 7–9). The nucleus of the functional (chalazal) macrospore then divides, the orientation of the spindle being in the direction of the long axis of the embryo sac (fig. 8), and a 2-nucleate macrogametophyte is formed (fig. 9). The second nuclear division, resulting in the formation of a 4-nucleate embryo sac, then occurs (figs. 10, 11), the orientation of the spindles in this case being transverse to the long axis of the embryo sac.

Meanwhile, the micropylar portion of the embryo sac has expanded laterally to a greater extent than the chalazal end, so that the embryo sac is more or less swollen toward the micropyle and tapers gradually toward the tubular chalazal end. The four nuclei divide again simultaneously (figs. 12, 13) to give rise to an 8-nucleate embryo sac. Three nuclei in the micropylar portion of the now greatly enlarged embryo sac become delimited by cell walls to form the egg apparatus, consisting of an egg cell and two synergids. Similarly, three of the chalazal nuclei become surrounded by cell walls to form the three antipodal cells in the narrow tubular portion of the embryo sac. The two remaining polar nuclei subsequently fuse to form the large primary endosperm nucleus of the mature 7-celled embryo sac (figs. 14, 15).

DISCUSSION

In macrosporogenesis and the development of the embryo sac, *Y. aloifolia* conforms in general to the "normal type" characteristic of the vast majority of angiosperms which have been investigated. The female gametophyte of *Y. aloifolia* is very similar to that of *Y. gloriosa* (Vesque 1879; Guignard 1882; Hérail 1889), *Y. filamentosa* (Reed 1903), *Y. glauca* (Folsom 1916), and *Y. rupicola* (Watkins 1937). Development of the embryo sacs of various species of *Yucca* seems to vary somewhat, however, in the

Explanation of figures 8–15

FIG. 8. Metaphase stage of first division in the embryo sac. × 480.

FIG. 9. 2-nucleate embryo sac. × 480.

FIG. 10. Telophase stage of second division in the embryo sac. × 360.

FIG. 11. 4-nucleate embryo sac. × 360.

FIG. 12. Prophase of third division in the embryo sac. × 360.

FIG. 13. Metaphase of third division in the embryo sac. × 360.

FIG. 14. 8-nucleate embryo sac, showing egg cell, two synergids, three antipodals, and the two polar nuclei. × 270.

FIG. 15. Mature 7-nucleate embryo sac; the two polar nuclei have fused to form the primary endosperm nucleus. × 270.
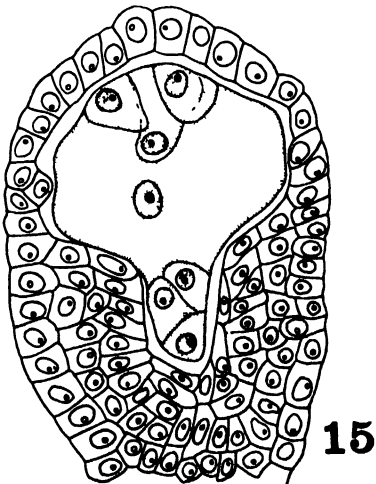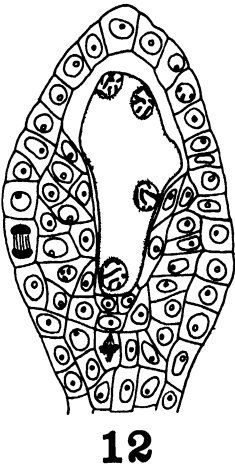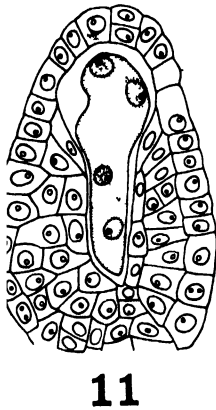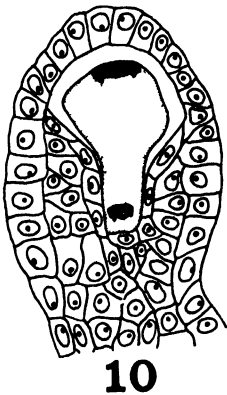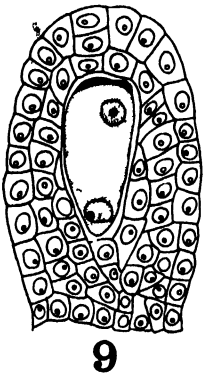
arrangement of the macrospores in the tetrad. It would appear that the failure of early investigators to note the formation of four macrospores may be due to the fact that the micropylar pair often lie side by side, the tetrad thus having a "T-arrangement." An axial row of four linearly arranged macrospores occurs regularly in *Y. filamentosa* according to Koernicke (1901) and Reed (1903), and in *Y. rupicola* according to Watkins (1937). In *Y. glauca,* Folsom (1916) reports that the "T-arrangement" is usual, but an axial row also occurs frequently. In *Y. aloifolia* also the "T-arrangement" appears to predominate.

Another point of variance among the various investigators has to do with the identity of the macrospore which becomes functional in the formation of the embryo sac. According to Folsom (1916), in *Y. glauca* any one of the tetrad of macrospores may develop. Guignard (1882) reported that either the chalazal macrospore or the one lying immediately above it could form the female gametophyte. In *Y. filamentosa,* Reed (1903) states that in every case in which he was certain, the macrospore next to the chalazal one proceeded to develop into the female gametophyte. Formation of the embryo sac in *Y. aloifolia* is in accord with the findings of Hérail (1889) and Watkins (1937) in other species; in every case observed, it is the chalazal macrospore which develops.

The chalazal tube of the mature female gametophytes of *Y. filamentosa* and *Y. rupicola* has been considered by Reed (1903) and Watkins (1937) as being haustorial in function. It would appear that *Y. aloifolia* is essentially similar in this respect. Raciborski (1893), apparently the only previous investigator to study the embryo sac in *Y. aloifolia,* found that as a result of staining with a fuchsin-iodine green combination the nuclei of the egg apparatus and the polar nuclei stain red, while the antipodal nuclei are blue-staining. An explanation of this difference in staining reaction probably has to do with a difference in function. Perhaps the suggested haustorial function of the chalazal portion of the embryo sac, including the antipodals, may explain Raciborski's observations.

SUMMARY

In *Yucca aloifolia* L. macrosporogenesis results in the formation of a tetrad of macrospores, generally with a "T-arrangement," the micropylar pair lying side by side. The chalazal macrospore is the one which becomes functional in the formation of the embryo sac. The development of the female gametophyte is of the "normal type," the embryo sac at maturity being 7-celled. The chalazal portion of the mature embryo sac is tubular, perhaps serving an haustorial function.

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LIGHT AND THE GROWTH OF EXCISED ROOTS OF DATURA

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(WITH ONE FIGURE)

In experiments on the growth of excised *Datura* roots performed in part with the assistance of Mary Bartley Schmidt in 1938, observations were made on the effect of light on their growth. Although the number of roots observed was small and they were grown in a limited number of solutions the results were quite definite and may be of interest to others working in this field.

The excised roots were obtained from seeds supplied by A. F. Blakeslee and came from an inbred line of diploid *Datura stramonium*, lot no. 3702564. Seeds were sterilized with calcium hypochlorite and germinated on sterile water agar.

On August 18, 1938, a 5 mm. terminal piece of a seedling root was transferred to 50 ml. of modified Pfeffer's solution containing 2 per cent Merck's maltose and 100 p.p.m. Harris yeast. The root was placed in diffuse light at 23°–24° C. On September 5, after 18 days growth, it had reached a length estimated to be about 12 cm., but had formed no branch roots.

It was noted at that time that tufts of root hairs occurred along the length of the root at more or less regular intervals. The root was somewhat thickened at the places of heavy root hair production. The appearance of the root at this time is shown diagrammatically in figure 1. Thirteen groups of
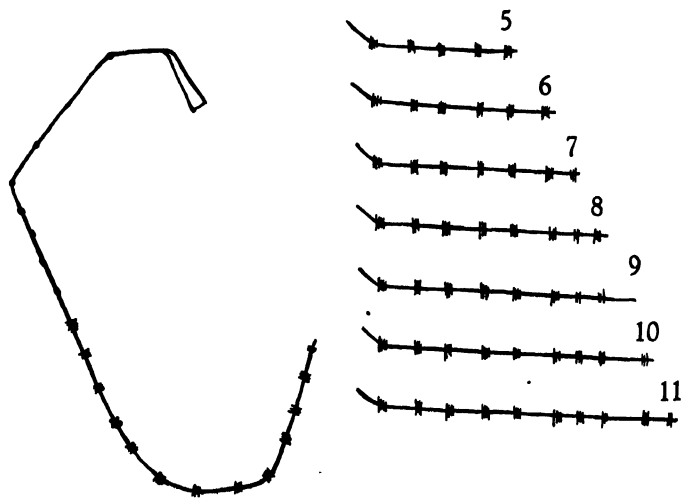
FIG. 1. Left, Excised *Datura* root after 18 days growth in diffuse daylight. Note tufts of root hairs at intervals. Right, Terminal portion of *Datura* root on September 5, 6, 7, 8, 9, 10 and 11. Kept in continuous darkness September 9. Note cluster of root hairs for each day except September 9.

root hairs from 3 to 6 mm. apart could be clearly seen and above these, nearer the base, were several swellings, some of which were the beginnings of branch roots.

Observations of the root were made daily, and it was found that a cluster of root hairs was produced each 24 hours during the daylight hours. Elongation occurred mainly at night, with short and scattered root hairs. During the daylight hours the root elongated slowly, thickened somewhat, and the root hairs found were long and close together. The development of the root on several successive days is shown in figure 1.

The relation of light to this phenomenon was confirmed by placing the root in a dark cabinet on September 8th. During the next 24 hours the root elongated, but no tuft of root hairs was found. The root was returned to the light on September 10th, and clusters of root hairs were formed on the 10th and 11th. Observations were discontinued at that time.

A second seedling excised root was grown in diffuse light in the maltose-yeast solution, and root hairs in tufts were noted, but no observations to relate the tufts to light and darkness were made. Subcultures of this root were grown in solutions containing thiamin and vitamin B_6, and as they developed in diffuse light the characteristic clustered root hairs appeared on parts of the root. Other portions developed thickenings at regular intervals, but few or no root hairs. The thickenings gave the root a beaded appearance and were assumed to be associated with alternate exposure to light and darkness.

It appeared, therefore, that growth in length of excised *Datura* roots under the conditions described was inhibited by exposure to light. With the inhibition of elongation a thickening of the root occurred, and frequently, though not always, long root hairs were produced freely on the thickened portion.

Unfortunately no microscopic studies were made which might have made clearer what occurred during the light period. It may be suggested, however, that when normal elongation was inhibited by light the internal pressure of the cells was not relieved by elongation and exerted its effect by increasing the crosswise diameter and pushing out the long root hairs. A similar explanation was offered for the failure of root hairs to develop on excised strips of the periblem and dermatogen of corn roots as contrasted to their development when the same tissues remained attached to the plerome (2).

A light effect of this character has not been reported for excised roots of other plants. Excised tomato roots seem unaffected by exposure to light (3, 4), and corn roots were stated by Robbins and Maneval (1) to be favorably influenced by light in some instances.

To speculate on how light produces its effect on the excised *Datura* root

is perhaps premature. Two obvious possibilities may be suggested. Light may produce inhibitors which are destroyed in darkness. This is not an unreasonable suggestion in view of the known facts of photosensitivity. On the other hand light may destroy growth substances formed in darkness and necessary for the elongation of cells. Auxins are destroyed by light and are concerned in cell elongation, but their relation to the elongation of roots is still somewhat obscure. If the second suggestion is correct, it would seem that the quantity of the growth substance in these roots is less than in tomato roots, for example, which do not appear to be sensitive to light; or that the conditions under which it exists in the *Datura* cells make it more sensitive to light than in tomato roots. Other possibilities could be suggested but their presentation will be delayed until more knowledge of the phenomenon is at hand.

THE NEW YORK BOTANICAL GARDEN
                    AND
DEPARTMENT OF BOTANY,
    COLUMBIA UNIVERSITY.

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SOME NUCLEAR PHENOMENA IN VENTURIA INAEQUALIS[1]

E. J. BACKUS AND G. W. KEITT

(WITH TWENTY-TWO FIGURES)

The development of the ascocarp of *Venturia inaequalis* (Cke.) Wint. has been studied by Killian (1917) and Frey (1924), both of whom reviewed extensive literature dealing with sexuality in the Ascomycetes. Their work has been reviewed by Keitt and Palmiter (1938) in connection with studies on heterothallism and variability in this fungus. Observations on the cytology of the imperfect stage of this organism have been reported by Wiltshire (1915) and Nusbaum and Keitt (1938) in studies on host-parasite relations. Recent work by Keitt, Palmiter, and Langford (1938) and Keitt and Langford (1940) on variability and inheritance of this pathogen make desirable further investigation of the development of the ascus and of nuclear phenomena in the vegetative mycelium, the conidiophore, and the conidium. Such studies are reported in the present paper.

MATERIALS AND METHODS

Overwintered leaves collected in March and April of 1938 and 1939 from apple orchards at Gays Mills, Wisconsin, and Sturgeon Bay, Wisconsin, constituted the source of material for this investigation. The leaves were placed outdoors on sod under wire cages for development of the asci (*cf.* Wilson, 1928). From time to time leaves were brought into the laboratory and placed in a moist chamber for a short period. Prior to fixation, microscopic examination was made to determine the stage of development of the asci.

Formal-acetic alcohol was most extensively used as a fixative and proved most successful, although Allen's modification of Bouin's mixture also gave a number of favorable fixations. Carnoy's A, Carnoy's B, Conant's, and Navashin's solutions were tried, but all gave unsatisfactory results. Paraffin infiltration was accomplished by the butyl alcohol technique. Slides were prepared from the embedded portions of leaf by cutting microtome sections 7–8 μ thick and staining with Heidenhain's iron-alum haematoxylin.

In addition to the cytological preparations made in the above manner, supplementary slides of another sort were prepared by teasing out fresh ascocarpic material and crushing it in cotton-blue and mounting fluid.

EXPERIMENTAL RESULTS

The Ascus. By the use of both stained paraffin sections and crushed fresh ascocarpic material, it was shown in confirmation of the work of Killian

(1917) that the asci of *Venturia inaequalis* are initiated by crozier formation. The crozier is formed when the tip of an ascogenous hypha bends and walls are formed in such manner as to make a uninucleate terminal cell and a binucleate penultimate cell. The nuclei of this cell fuse almost as soon as it is formed. Such a crozier with its fusion nucleus is shown in figure 1. This sub-terminal cell grows and develops into the young ascus. The primary ascus nucleus is large in proportion to the size of the cell, having a diameter equal to more than three-fourths that of the ascus at this stage. A large nucleolus and considerable amounts of darkly-staining chromatic material are observed. Very conspicuous beads of chromatin are present on the thin threads which wind throughout the nuclear cavity (fig. 2).

The ascus soon elongates and the nucleus divides. Figures 3–6 show examples of the first division. The spindle is intranuclear, at least a portion of the old nuclear membrane usually being visible. There appears characteristically to be a darkly-staining granule at each end of the spindle. It is suggested that these granules are probably centrosomes. The chromosome number here is questionable. Although some figures would suggest that four is the haploid number (fig. 5), others would seem to indicate that it may be as high as six. As the telophase stage is reached, the figure is marked by the persistent spindle which extends between the two groups of chromosomes at the poles, and by the presence of a granule in the cytoplasm adjacent to it (fig. 6). This granule is thought to be the remains of the nucleolus. With the exception of one figure in which the spindle appeared to be in a more or less transverse position, spindles in the first division were found to extend longitudinally in the ascus.

After this first division has been completed, two nuclei which appear to be about one-fourth as large as the primary nucleus are formed. Although there is decidedly less chromatin visible, the same beaded effect mentioned above is again in evidence here (fig. 7). The second division was observed

Explanation of Figures 1–11

(All figures were drawn with the aid of an Abbe camera lucida at a magnification of about 1740 diameters.)

FIG. 1. Crozier showing fusion nucleus in the penultimate cell and the disintegrating terminal cell.

FIG. 2. Young ascus with large primary nucleus in late prophase.

FIGS. 3–4. Stages in first nuclear division showing chromosomes at the mid-plane of the intranuclear spindle. Note the centrosomes at the spindle poles.

FIG. 5. Early anaphase of the first nuclear division.

FIG. 6. Telophase of the first nuclear division showing persistent spindle and remains of the nucleolus.

FIG. 7. Binucleate ascus.

FIG. 8. Second division in the ascus at equatorial plate stage.

FIG. 9. Telophase of the second division.

FIG. 10. Newly organized nuclei following completion of the second division.

FIG. 11. Four-nucleate ascus.
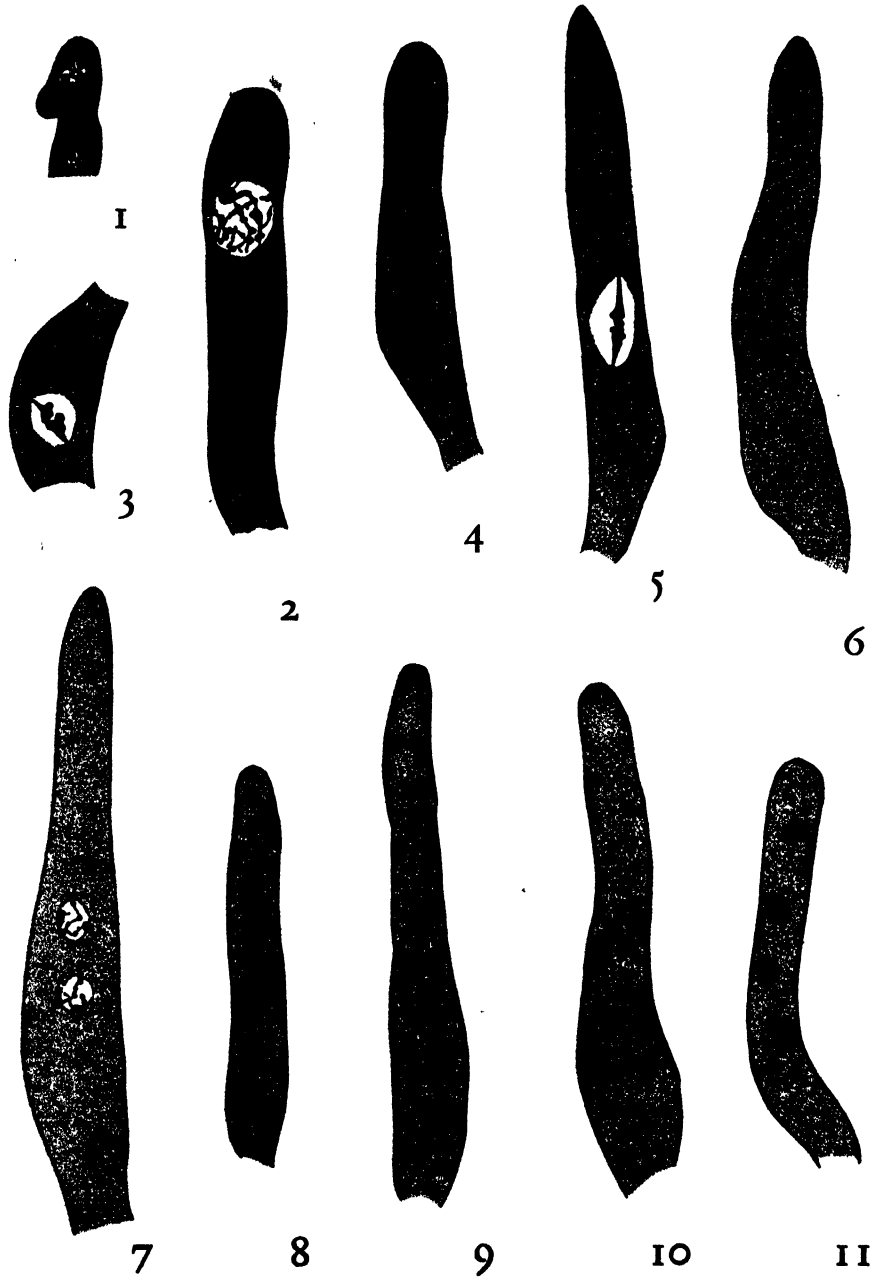
in a considerable number of asci. Although the general form of the figure appeared to be about the same as in the first division, there seemed to be a considerable variation in the orientation of the spindles. Apparently they may take any of three positions in the ascus with equal frequency, being longitudinal, oblique, or nearly transverse (figs. 8–10). Here again it is not possible to be sure of the chromosome number. Figure 9 shows the second division in telophase with the persistent spindles and the darkly-staining granules in the cytoplasm beside them.

Four nuclei are formed after this second division, and a further reduction in size as compared with the binucleate ascus is noted. The beaded appearance of the chromatic network is still present but not so conspicuously as in the larger nuclei (fig. 11). The third division was the most difficult to find, which suggests that it takes place very rapidly and that there is a comparatively short lapse of time between the four-nucleate and the eight-nucleate stages. Spindle orientation is most variable in the third division, as evidenced by figures 12 and 13, which show the spindles as being vertical, oblique, and transverse. The general form of the figure here is again the same as that described for the earlier divisions.

The third division results in the formation of eight free nuclei. They were observed many times occupying a position in a line down the middle of the long, narrow ascus (fig. 15). Asci were found that showed the eight nuclei in a peripheral position, probably just prior to spore formation. The nuclei are somewhat smaller than in the four-nucleate stage, and they show a less definite chromatic network.

From the preparations studied little that was definite could be learned as to the manner in which the spores are delimited, although the presence of beaked nuclei and astral radiations was suggested in a few asci. The sections studied likewise gave evidence suggesting that the spores are delimited as rounded structures which later elongate. Crushed perithecia stained with cotton-blue also showed asci with spores whose shape supports the idea that they are cut out round. The scarcity of these stages in the sections may be attributed in part to the very short time that the spores retain this spherical shape.

When first formed, the spores are uninucleate. Although no satisfactory preparation was obtained showing a nuclear division in the young spores, it can not be doubted that such a division takes place, since each spore ultimately contains two nuclei. This division takes place shortly after the spore is formed and while it is still somewhat spherical. Figure 16 shows an ascus that contains both uninucleate and binucleate spores. A septum is barely discernible in the apical spore. This ascus is noteworthy from two other standpoints. First, it illustrates the fact that the two cells of the spore are approximately equal in size when first formed. Second, it shows that the spores while still unelongated may come to lie side by side. When they again

become uniseriate it is possible that changes from the original serial order may occur. It would seem likely that spores that lie beside each other would either resume their original positions when the ascus elongates or else exchange their original positions. In the ascus shown in figure 16 it appears that sister spores do not lie beside each other, and if the original position were exchanged this fact would be detectable by culturing the spores in their serial order and studying the characters of the isolates. In the ascus shown in figure 18, however, it would appear that sister spores do lie beside each other, and no significance would attach to their possible exchange of position because they are identical twins.

The further elongation of the spores, and the unequal growth in size of the two cells of each spore, which is characteristic of this genus, are the next changes to be observed in the development of the ascus (figs. 17–18). The spores at this time stain more darkly, and a heavier wall begins to be formed. They usually come to fill the greater portion of the ascus, which has grown to keep pace with the enlarging spores. By the time the ascus is mature most of the epiplasm has disappeared and the ascus wall stains faintly. The mature spores, which average 12–15 µ in length, have a heavy, olivaceous wall.

The Mycelium. An investigation of the cytology of the mycelium was accomplished by the preparation of stained microtome sections of fixed blocks of an agar medium upon and through which the fungus had grown. It was found to be branching, septate, and composed of uninucleate cells (fig. 19). Although there was considerable variation in the cells, both as to length and width, no cell of the mycelium was ever found to contain more than one nucleus.

The Conidiophore and the Conidium. Fresh apple leaves parasitized by *Venturia inaequalis* were collected in September of 1939. Slides which revealed the cytological structure of both the conidia and the conidiophores were prepared by scraping portions of the conidial mats from the leaves into a drop of egg albumen on a slide, adding a small drop of fixative, drying,

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Explanation of Figures 12–22

Figs. 12–13. Equatorial plate and telophase stages of the third division. Note irregularity in spindle orientation.

Fig. 14. Stage following completion of the third nuclear division.

Fig. 15. Eight-nucleate ascus.

Fig. 16. Ascus containing both uninucleate and binucleate spores. Note septum in the apical spore.

Fig. 17. Ascus showing slightly elongated binucleate spores prior to septation.

Fig. 18. Ascus with spores elongated, septate, and showing beginnings of uneven growth of the two cells.

Fig. 19. Mycelium showing uninucleate cells.

Figs. 20–21. Conidia and conidiophores with uninucleate cells.

Fig. 22. Uninucleate conidium.

12 13 14 15 16
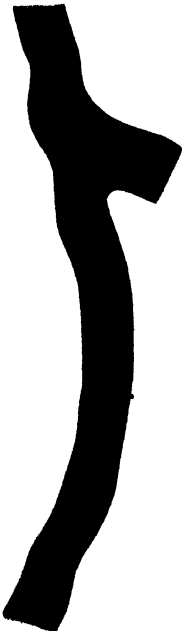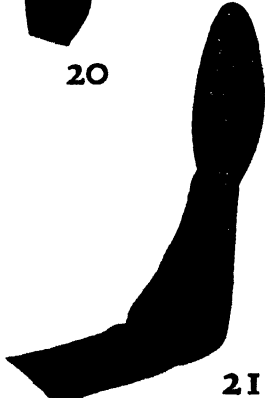
17 18 19 20 22 21

rinsing in water, and staining with Heidenhain's haematoxylin. It was found that the cells of both the conidiophores and the conidia are always uninucleate. The nuclei, which are comparatively large, show a rather distinct chromatin reticulum within the nuclear membrane (figs. 20–22).

<div align="center">DISCUSSION</div>

Relations of position of the spindles in nuclear divisions in the ascus to the serial order of arrangement of the ascospores and phenomena of inheritance have been studied in *Neurospora* by Dodge (1927, 1936), Wilcox (1928), and Lindegren (1932).

In the first nuclear division in the ascus of *Venturia inaequalis* the spindle is oriented longitudinally in the ascus. In the second and third nuclear divisions the spindles may be longitudinal, oblique, or nearly transverse. Following the third division the nuclei are found in a line down the middle of the ascus. After the ascospores are delimited they frequently show a more or less biseriate arrangement, but become uniseriate again when the ascus elongates prior to dehiscence.

The longitudinal orientation of the spindle in the first nuclear division places the daughter nuclei in such position that, barring nuclear or spore migration, the four ascospores that derive their nuclear complements from each will lie at opposite ends of the ascus. The position of the spindles in the second and third nuclear divisions is ordinarily such that the sister nuclei will be arranged in pairs in the serial order of occurrence of nuclei from base to apex of the ascus. However, an ascus was observed, as is shown in figure 13, in which the position of the spindles would suggest the possibility of a departure from perfect pairing. Furthermore, in asci in which the ascospores temporarily assume a biseriate arrangement, there would seem to be some possibility for change from the original serial order of spores when the ascus elongates. These results, which have much similarity to those reported by Wilcox (1928) for *Neurospora sitophila,* are in accord with the findings of Keitt, Palmiter, and Langford (1938) and Keitt and Langford (1940) on the relation of serial order of arrangement of the spores in the ascus to their inheritance. Further studies of variability and inheritance of this organism are being made by Keitt and Langford, and it is projected that these will be discussed in relation to the cytological phenomena herein reported.

The fact that the cells of the vegetative mycelium, the conidiophore, the conidium, and the ascospore are uninucleate is of much significance in relation to genetic studies of this organism, as this would seem to preclude the possibility of variability due to heterocaryosis.

<div align="center">SUMMARY</div>

The asci of *Venturia inaequalis* arise from croziers near the base of the ascocarp. The primary ascus nucleus is large and shows prominent chro-

matin beads. Three successive nuclear divisions in the ascus result in the formation of eight nuclei. The spindles in the first division are oriented longitudinally in the ascus, while those of the second and third are longitudinal, oblique, or nearly transverse. The position of the spindles is such that after each division the sister nuclei ordinarily are arranged in pairs in the serial order of occurrence of the nuclei from base to apex of the ascus. Barring nuclear or spore migration, the four spores in either end of the ascus should ordinarily derive their nuclear complements from one first-division nucleus. It appears that sister spores ordinarily lie next to each other in the ascus. The spores seem to be delimited as spherical structures. They are at first uninucleate, but a nuclear division followed by a cell division soon occurs and each spore is then composed of two uninucleate cells of equal size. The spores then elongate rapidly, the two cells of each growing unequally. The cells of the vegetative mycelium, the conidiophore, and the conidium are uninucleate.

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A NOTE ON SAPIUM

JOSEPH MONACHINO

During the course of routine identification work in the herbarium of the New York Botanical Garden some studies were undertaken on a certain group of the genus *Sapium*. These studies have revealed the desirability of transferring three specific names to varietal rank, and have brought to light a hitherto undescribed variety.

SAPIUM BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **nitidum** Monachino, var. nov. Haec varietas a forma typica speciei recedit foliis manifeste alternis nitidis obovatis usque ad ellipticis integris, ad apicem complanatis; glandis petiolorum brevibus, in petiolo sitis; spicis singulis terminalibus tenuibus elongatis; capsulis pedicellatis glabris.

This variety differs from the typical form of the species in its leaves being manifestly alternate, shining, obovate to elliptic, entire, with flat tips; petiolar-glands short, on the petioles; spikes single, terminal, slender, elongated; capsules pedicellate, smooth.

Stipules small, ovate to oblong, acutish or blunt at apex; petioles slender, 1–3.5 cm. long, their glands borne at the apex, short; leaf-blades shining when mature, obovate to oblanceolate or elliptic, 3–13 cm. long, 1.5–5 cm. wide, acute at base, extending down the petiole and becoming sulcate between the glands, typically short-acuminate and blunt (or merely rounded) at the apex, without a reflexed or unguiform acumen; prominent primary veins relatively few and distant (6–15), curved and running parallel with the leaf-margins; edge of leaf-blade with a narrow cartilaginous rim, entire (in the type); staminate spikes solitary, terminal, slender, up to 15 cm. long; glands on the rachis long and narrowly oblong, with their ends curving upwards from the rachis or raised; capsules distinctly pedicellate (the pedicels 2–4 mm. long), smooth, up to 8 mm. long and wide, composed of 2 cocci (in the type), 2-valved, each valve splitting again about ¾ of the distance to the base, with thin edges, the cell-partitions remaining on the central axis after dehiscence; seeds about 6 mm. long and wide, coated with a red pseudo-aril.

BRITISH HONDURAS: on deep river-alluvium, Santa Rosa Pasture, 2 miles from El Cayo, alt. 65 m., *J. B. Kinloch 340*, May 28, 1940, TYPE; in the Britton Herbarium of the New York Botanical Garden.

Kinloch gives the following additional information about the variety: a common tree in both alluvium and limestone soils, to 60 feet tall; trunk diameter to 24 inches; bark smooth, gray; crown dense and spreading; latex white, rubbery, abundant; with the general habit of *Ficus radula*. The leaves have a dark-green petiole and red-tinged midrib when fresh, their margins crenulate. The fruit is a 2-celled capsule.

Many of the species of the genus *Sapium* are not only extremely variable in themselves, but also approximate closely related species in such an intergrading manner that separate units can be recognized only by the use of

composite characters. Any single diagnostic or "key" character, such as venation, shape, size, and position of petiolar glands, and leaf-apices, or the singularity or plurality of inflorescence-spikes, is far too variable to be categorically accepted as a means for identification. In a plant group of such disposition the author believes that the nomenclatural designation of "variety" is the more modest and accurate designation for the entities or nuclei of complexes, and that a treatment such as that of Müller in De Candolle's *Prodromus*, where the species *S. biglandulosum* is given more than a dozen varieties (and can easily be made to include twice as many), is preferable to the more rigid binomialism of Pax in *Das Pflanzenreich*. Not even Pax could entirely refrain from varietalizing, since, for instance, he recognized nine distinct varieties of *S. marginatum*. Only because of this belief does the present writer relegate the new plant from British Honduras, described above, to varietal rank; for, otherwise, as species in Pax's treatment go, it would certainly merit the status of a separate species.

It is perhaps also worthy of mention that when *Kinloch 340* was entrusted to the writer for identification, the fact that it was a *Sapium* from British Honduras led him to consult Standley & Record's publication on the flora of that country. The only species therein recorded, *S. jamaicense* Sw., is represented in the Britton Herbarium by specimens from Panama, Costa Rica, and Guatemala. Two additional specimens labeled *"Sapium jamaicense,"* from Central America, resemble each other closely, but are obviously incorrectly determined. Their leaves have well-developed apical glands. Plate 17 in volume 12 of Contributions from the United States National Herbarium (1908) fits them perfectly. This plate represents SAPIUM BIG-LANDULOSUM (Aubl.) Müll.-Arg. var. **oligoneurum** (K. Schum. & Pittier) Monachino, stat. nov. (*Sapium oligoneurum* K. Schum. & Pittier, Contrib. U. S. Nat. Herb. **12**: 168, *pl. 17*. 1908). One of the specimens, from a staminate plant, is from the republic of Honduras; the other (*W. A. Schipp 1049*), a fruiting specimen, is from British Honduras. Its pedicellate capsules and other characters fit the original description of S. BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **sulciferum** (Pittier) Monachino, stat. nov. (*Sapium sulciferum* Pittier, Contrib. U. S. Nat. Herb. **12**: 169, *f. 10*. 1908). On the other hand, in *Das Pflanzenreich*, volume IV, 147⁵ (1912), *"S. sulciferum"* is included in the "Clavis specierum" under the heading "A. Capsula sessilis, non stipitata," and Schipp's specimen in that key would come out as SAPIUM BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **bogotense** (Huber) Mona-chino, stat. nov. (*Sapium bogotense* Huber, Bull. Herb. Boiss. (II) **6**: 355, *f. 13*. 1906). Under the circumstances it is not possible to definitely identify these two specimens and a final statement of their identity must await comparison with the type specimens of the above-mentioned varieties.

THE NEW YORK BOTANICAL GARDEN,
    NEW YORK, NEW YORK.

BREEDING WORK TOWARD THE DEVELOPMENT OF A TIMBER TYPE OF BLIGHT-RESISTANT CHESTNUT. REPORT FOR 1939[1]

Arthur Harmount Graves

The purpose of this work is to develop, by breeding, a type of chestnut tree of tall straight growth, and at the same time, resistant to the blight fungus, *Endothia parasitica* (Murr.) P. J. and H. W. And. It is generally known that this fungus, inadvertently introduced from Asia more than 40 years ago, has now practically exterminated the American chestnut (*Castanea dentata*) at least so far as its value as a forest tree is concerned.

Ten years ago[2] we began breeding the American chestnut with an oriental species, *Castanea crenata,* the Japanese chestnut. That species has considerable resistance to the attack of the blight fungus, but is a comparatively low growing tree, quite unsuitable for replacing the American tree species as a timber tree in our Eastern forests.

In general, the first generation of Japanese-American hybrids has shown dominance of the American species, as evidenced by the erect habit of growth and by the leaf characters. However, the dominance is not complete. This is shown by the fact that the susceptibility to the blight is not so great as that of the American parent. In order to introduce greater resistance into the stock, it has been our policy to cross these Japanese-American hybrids again with resistant Japanese and with resistant Chinese, with the result that we now have 93 trees of (*C. crenata* × *C. dentata*) × *C. crenata* or the reciprocal, and 8 of (*C. crenata* × *C. dentata*) × *C. mollissima,* growing on our plantation. We have also intercrossed these F_1's (*C. crenata* × *C. dentata*) in the hope of developing forms with a greater content of Japanese stock. At present we have 139 of these F_2's. Many other crosses have been made (see table 2) and representatives of most of these are now growing on the trial grounds, where they are being tested for disease resistance by our inoculation method. These are located at the eastern end of the Sleeping Giant Mountain, Hamden, Connecticut.

Cooperative Planting. In 1939 we continued to extend our cooperative plantations, and accordingly supplied seedlings to Dr. D. F. Jones, of the Connecticut Agricultural Experiment Station at New Haven, for planting on the experimental farm of the Station at Mt. Carmel, Hamden, Conn.

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[1] Brooklyn Botanic Garden Contribution No. 92.

[2] Recent annual reports have been published in the Brooklyn Botanic Garden Record as follows. For 1929, Brooklyn Botanic Garden Record 19: 62–67; for 1930, 20: 83–87; for 1931, 21: 46–53; for 1932, 22: 57–63; for 1933, 23: 67–75; for 1934, 24: 59–65; for 1935, 25: 62–75; for 1936, 26: 47–60; for 1937, 27: 44–55; for 1938, 28: 54–60; for 1939, 29: 58–63.

The trees now growing here, as well as in the two other cooperative plantations already established, are shown in table 1.

TABLE 1. COOPERATIVE PLANTATIONS
Cooperative Plantation No. 1
On Farm of Dr. W. W. Herrick, Sharon, Conn.
Seedlings in first year of growth ; from nuts harvested in 1938

C. crenata × C. dentata	2
C. crenata × (C × D)[1]	10
(C × D) × C. crenata	3
(C × D) × (C × D)	8
C. mollissima × C. dentata	2
C. mollissima × (C × D)	14
C. Seguinii × C. crenata	1
88 × C. dentata	4
88 × C. mollissima	6
88 (from open pollination) 2 years old	75
Total	125

Cooperative Plantation No. 2
On Grounds of New Haven Water Company, Orange, Conn.
All seedlings in first year of growth ; from nuts harvested in 1938
Seedlings from open pollinations

C. crenata × C. dentata	119

Seedlings from controlled pollinations

C. crenata × (C × D)	6
C. Seguinii × C. mollissima	3
C. mollissima × (C × D)	1
Total	129

Cooperative Plantation No. 3
On Farm of Connecticut Agricultural Experiment Station ; Mt. Carmel (Hamden), Conn.
All seedlings in first year of growth ; from nuts harvested in 1938

C. mollissima × C. crenata	3
C. mollissima × (C × D)	3
C. crenata × C. mollissima	3
C. crenata × C. dentata	7
Total	16

[1] C × D = C. crenata × C. dentata.

Hybrids of 1939. The following is a brief account of the chestnut hybridization work in 1939. Since I was absent in England and Scotland during most of the period, the direct supervision of the work was in charge of my assistant, Miss Hester M. Rusk. As has been our practice since 1935, all the cross pollinations were made on trees growing at the plantation at Hamden, Connecticut. In the following list, as is customary, the name of the female parent is given first. The combinations with an asterisk are new to science. The numbers in parentheses at the left of certain combinations correspond with the numbered notes which follow.

(1) Most of these are crosses of our most resistant Japanese with valuable American pollen sent us by Mr. J. C. McDaniel of T.V.A., Norris, Tennessee, and by Mr. H. F. Stoke of the Mountain Nut Co., Roanoke, Virginia.

(2 and 3) Include a large number of crosses with our best Japanese American hybrids and our most resistant Japanese and Chinese individuals —145 nuts in all.

(4) In 1932 I secured nuts of the Spanish chestnut, C. *sativa*, from several European Gardens. The resulting seedlings have been particularly

TABLE 2. HYBRIDS OF 1939

No. of nuts

(1) *C. crenata* × *C. dentata* 88
    C. crenata × (*C* × *D*) 130
    **C. crenata* × *C. neglecta*[1] 13
    C. crenata × (*C. mollissima* × *C. Seguinii*) 31
(2) (*C* × *D*) × *C. crenata* 124
(3) (*C* × *D*) × *C. mollissima* 21
(4) *(*C* × *D*) × *C. sativa* 5
    (*C* × *D*) × (*C* × *D*) 21
    S8[2] × *C. crenata* 15
    S8 × *C. mollissima* 16
    S8 × (*C* × *D*) 54
    (*S8* × *C. crenata*) × *C. dentata* 3
    *(*S8* × *C. dentata*) × *C. crenata* 2
    *(*S8* × *C. dentata*) × (*C. crenata* × *C. dentata*) 5
    (*S8* × *C. dentata*) × *S8* 21
    (*C. crenata* × *S8*) × *C. crenata* 21
    **C. dentata* × *C. neglecta* 6
    *(*C. dentata* × *S8*) × *C. crenata* 2
    *(*C. dentata* × *S8*) × *S8* 4
(5) *C. mollissima* × *C. dentata* 41
    C. mollissima × (*C* × *D*) 29
    C. mollissima × *S8* 3
    **C. mollissima* × (*C. crenata* × *S8*) 10
(6) **C. mollissima* × [(*C* × *D*) × (*C* × *D*)] 34
    C. mollissima × (*C. mollissima* × *C. dentata*) 7
    *[(*C. mollissima* × *C. pumila*) × *C. dentata*] × *C. crenata* .. 3
    (*C. mollissima* × *C. Seguinii*) × *C. crenata* 35
    (*C. mollissima* × *C. Seguinii*) × *C. dentata* 12
    **C. Seguinii* × (*C* × *D*) 11

    Total 767

[1] *C. neglecta* is a cross of *C. pumila* and *C. dentata*.
[2] *S8*, one of the Van Fleet hybrids, is apparently a combination of *C. crenata* and *C. pumila*. The "*S8*'s" in our plantation are from open pollinated seedlings of *S8*. For "*C* × *D*" see note to table 1.

unpromising because (1) they die back in the winter and (2) they proved very susceptible to the blight. On the other hand, the growth has been vigorous, with thicker, stronger, and longer shoots than in any other species. It is on account of this valuable growth character that we are trying to incorporate this stock into our hybrids.

(5) One of our best Chinese crosses with *C. dentata* pollen from a seedling raised by us from a nut planted in 1926. The tree from which this nut came was a large specimen near Portland, Maine. This young seedling American, however, is now badly blighted.

(6) A cross of two Japanese American hybrids, four years old, made in 1935, bloomed for the first time this year and was crossed with one of our best Chinese. This, therefore, represents the beginning of the third generation in a time interval of only eight years, and is particularly important as evidence of the short time required for breeding experiments with the chestnut. *Castanea dentata* blooms at the age of about 12 years, most of the Japanese forms at about 5 years. We have heard of Chinese individuals blooming at the age of one year. We have had hybrids blooming and bearing nuts in their first year!

Testing for Disease Resistance by Inoculation with Endothia. This method, begun in 1936, was not continued last year on account of my absence in Europe, but may be resumed in 1940. By inoculation in the past, we have learned what are the most desirable individuals to use for breeding work, from the point of view of disease resistance. The method in use has already been described.[3]

[3] Report of the 28th Annual Meeting of the Northern Nut Growers Association, 1938: 97.

Hybrid Combinations New to Science. In the progress of this cross pollination from year to year new hybrids have been developed. It is our purpose, as soon as all the floral characters appear, to publish descriptions of the more important of these.

The following is merely a list of the new hybrids, a revision of that published early in 1939,[4] and includes the new combinations made by us in 1939.

TABLE 3.   NEW CHESTNUT HYBRIDS OF THE BROOKLYN BOTANIC GARDEN 1934–1939

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          Castanea crenata × C. neglecta—1939
          (C × D¹) × C. dentata—1934
¹ See note to table 1.
          (C × D) × C. mollissima—1935
          (C × D) × C. sativa—1939
          (C × D) × C. Seguinii—1936
          (C × D) × SS²—1936
² See note 2 to table 2.
          (C × D) × (C. mollissima × C. Seguinii)—1937
          (C × D) × (SS × C. dentata)—1938
          SS × C. sativa—1937
          SS × (C × D)—1936
          SS × (C. crenata × SS)—1937
          (SS × C. crenata) × C. dentata—1938
          (SS × C. crenata) × C. mollissima—1938
          (SS × C. dentata) × C. crenata—1939
          (SS × C. dentata) × (C. crenata × C. dentata)—1939
          (SS × C. dentata) × (SS × C. dentata)—1938
          C. dentata × C. neglecta—1939
          (C. dentata × SS) × C. crenata—1939
          (C. dentata × SS) × SS—1939
          C. mollissima × (C × D)—1935
          C. mollissima × (C. crenata × SS)—1939
          C. mollissima × [(C × D) × (C × D)]—1939
          (C. mollissima × C. crenata) × C. sativa—1937
          (C. mollissima × C. pumila) × C. dentata—1934
          [(C. mollissima × C. pumila) × C. dentata] × C. crenata—1939
          [(C. mollissima × C. pumila) × C. dentata] × (C × D)—1938
          (C. mollissima × C. Seguinii) × C. crenata—1937
          (C. mollissima × C. Seguinii) × C. dentata—1938
          (C. mollissima × C. Seguinii) × C. sativa—1937
          (C. mollissima × C. Seguinii) × (C × D)—1937
          (C. mollissima × C. Seguinii) × (C. mollissima × C. Seguinii)—1937
          C. Seguinii × C. alabamensis—1938
          C. Seguinii × C. dentata—1937
          C. Seguinii × C. pumila—1937
          C. Seguinii × C. sativa—1937
          C. Seguinii × (C × D)—1939
```

The following list of trees growing at the trial grounds at Hamden is presented to show not only what forms we now have under cultivation, but also, as indicated by the numbers at the right, the relative importance accorded to each species, variety or hybrid. For instance, *Castanea dentata,* the American chestnut, is represented by 100 trees, which have been grown from nuts sent us from many states throughout the range of the chestnut, from Maine to North Carolina. Different degrees of disease resistance occur in different strains and even individuals of *Castanea*. For this reason nuts of the American chestnut are much desired for planting. Without going into further detail, we let the list speak for itself.

Acknowledgments. As noted in the report of the work last year, the American Association for the Advancement of Science, in December, 1938, awarded us a grant-in-aid for the continuance of the work during 1939.

[4] Since the publication of this list in 1939, we have had access to unpublished records of the U. S. Department of Agriculture, and find that some of the combinations published by us as new had already been made by the Division of Forest Pathology, U.S.D.A.

TABLE 4.　CHESTNUT SPECIES, VARIETIES, AND HYBRIDS GROWING AT HAMDEN, CONNECTICUT
OCTOBER, 1939

Name	Number of Trees
Castanea alnifolia—Alder-leaved Chinquapin	4
C. Ashei—Ashe Chinquapin	2
C. crenata—Japanese Chestnut	53
C. dentata—American Chestnut	100
C. Henryi—Chinese Timber Chinquapin	13
C. Margaretta	1
C. mollissima—Hairy Chinese Chestnut	96
C. mollissima Mammoth—Chinese Chestnut var.	1
C. ozarkensis—Ozark Chinquapin	11
C. pumila—Chinquapin	32
C. sativa—Spanish Chestnut	55
C. Seguinii—Chinese Dwarf Chinquapin	16
S8 (C. crenata × C. pumila)	2
C. crenata × C. dentata	78
C. crenata × C. mollissima	6
C. crenata × S8	5
C. crenata × (C × D)	43
(C × D) × C. crenata	50
(C × D) × C. dentata	11
(C × D) × C. mollissima	8
(C × D) × (C × D)	139
(C × D) × (C. mollissima × C. Seguinii)	1
(C. crenata × S8) × (C. crenata × S8)	1
C. dentata × C. mollissima	12
C. dentata × S8	10
C. mollissima × C. crenata	2
C. mollissima × C. dentata	57
C. mollissima Mammoth × *C. dentata*	8
C. mollissima × C. pumila	1
C. mollissima × C. Seguinii	4
C. mollissima × S8	7
C. mollissima × (C. crenata × C. dentata)	152
C. mollissima Mammoth × *(C. crenata × C. dentata)*	8
(C. mollissima × C. crenata) × C. sativa	1
(C. mollissima × C. pumila) × C. dentata	7
(C. mollissima × C. Seguinii) × C. crenata	4
(C. mollissima × C. Seguinii) × C. mollissima	3
(C. mollissima × C. Seguinii) × C. sativa	1
(C. mollissima × C. Seguinii) × (C. mollissima × C. Seguinii)	2
(C. mollissima × C. Seguinii) × [C. sativa × (C × D)]	1
C. Seguinii × C. alabamensis	3
C. Seguinii × C. crenata	1
C. Seguinii × (S8 × C. dentata)	1
S8 × C. crenata	7
S8 × C. dentata	20
S8 × C. mollissima	30
S8 × C. sativa	16
S8 × C. Seguinii	9
S8 × (C. crenata × C. dentata)	3
(S8 × C. crenata) × C. dentata	11
(S8 × C. dentata) × (C. mollissima × C. dentata)	4
Stoke Hybrid No. 1, grafted on *C. mollissima*	2
Stoke Hybrid No. 1, grafted on *C. crenata*	2
Stoke Hybrid No. 2, grafted on *C. mollissima*	3
Stoke Hybrid No. 2, grafted on *C. crenata*	1
Stoke Hybrid No. 3, grafted on *C. mollissima*	2
Stoke Hybrid No. 4, grafted on *C. mollissima*	2
Various seedlings from "open pollinations"	54
Chinese and Japanese seedlings from open pollinations (approximately)	750
Total	1929

We acknowledge with pleasure the continued cordial cooperation of the Division of Forest Pathology, Bureau of Plant Industry, Washington, D. C. Many institutions and individuals, e.g., the Garden Club of America and the Connecticut Forest and Park Association, have granted us valuable assistance with offers of land for additional plantings and by sending us pollen and nuts of various species. A list of the donors of pollen and nuts is printed in the Annual Report for 1939 of the Brooklyn Botanic Garden, pages 56–59.

BROOKLYN BOTANIC GARDEN,
. BROOKLYN, NEW YORK.

A REVISION OF "LAURENTIA" AND ALLIED GENERA IN NORTH AMERICA

Rogers McVaugh

The genus *Laurentia* (Campanulaceae, Lobelioideae) was founded by Petro Antonio Micheli in 1729,[1] and included the single species known to him, a native of the Mediterranean region, the plant now called *L. Michelii* A. DC. Numerous other species have been described from southern Europe, tropical and subtropical Africa, western United States, Mexico, the West Indies, and Australia. At the present time there is considerable confusion as to the generic limits and as to the distinctions between *Laurentia* and related genera.

The genus *Laurentia*, as originally understood, and as delimited by authors generally as late as the publication of Bentham and Hooker's *Genera Plantarum* (1876), included a group of herbaceous, blue-flowered species with the corolla-tube lacking the dorsal slit that characterizes the genus *Lobelia*, with the ovary almost or wholly inferior, and with the filaments usually loosely adherent to the corolla-tube. The character that separates this genus from *Lobelia* is that the corolla in *Laurentia* is not at all divided on the side between the two narrow dorsal lobes, while in *Lobelia* it is slit to the base or very nearly so. Such a character appears to be scarcely of generic value, even in the Lobelioideae, where there prevails such uniformity of floral structure that no other sort of character is available.

Professor F. E. Wimmer of Vienna, the greatest living authority on the Lobelioideae, states[2] that the group as a whole contains about 1,000 species, distributed among 23 genera. Of these more than 800 belong to the four genera, *Burmeistera*, *Centropogon*, *Siphocampylus*, and *Lobelia*. Among all these 23 genera and 1,000 species, there are a few only that are separated by strong morphological characters; *Downingia*, for example, has the capsule dehiscent by lateral slits instead of by apical valves, and is quite distinct from all other genera. Another example is *Lysipomia*, an Andean genus of about 15 species, in which the capsule opens by an operculum. The number and disposition of the floral parts are identical in all the species of the subfamily, save those mentioned above and a few others. The taxonomist, as a consequence, has to fall back on relative characters such as the thickness or fleshiness of the hypanthium or the depth of the sinuses of the corolla. Such characters, while fairly satisfactory in any given small geographic area or when a small number of species is under consideration, usually break down

[1] Nov. Gen. Pl. t. 14. 1729.

[2] Campanulaceae, in Macbride, Flora of Peru. Field Mus. Publ. Bot. 13 (6): 383–489. 1937.

when applied to large series of species from all parts of the earth. As Gleason has pointed out[3] it would be perfectly feasible to unite the genera *Burmeistera, Centropogon,* and *Siphocampylus* into one vast genus without overstepping the bounds of logic. It would be equally possible to add to this genus the present genera *Lobelia, Laurentia,* and *Isotoma.* The principal objection to such a course is, in my opinion, a practical one. The limits of genera of the sort here considered are determined by convention and usage as well as by severe logic. The name-changes involved in such a step as that discussed above would be many, and much confusion and unnecessary synonymy would result.

It appears, then, that almost any attempt at a natural classification of the Lobelioideae must strike a balance among the following courses: (1) Define a considerable number of small genera, each fairly uniform in character, but set off from closely related groups by purely arbitrary characters. This course involves the creation of a number of new names. (2) Make generic limits ample enough to allow for the inclusion of most of the anomalous species. This will tend to make the genera larger and fewer, and will also necessitate the creation of many new names. (3) Make the genera as small and homogeneous as is compatible with logic, at the same time recognizing the weight of convention as it bears on the subject of generic limits. It seems to me that best results may be obtained from this last course, if at the same time it be remembered that the "genus", *as ordinarily defined*, is a conventional concept; it is less a natural unit than the species and more to be thought of as a means of classification. Convenience, therefore, must be taken into account as well as apparent kinship between species or groups. A single example will serve to illustrate this point. The plant known as *Lobelia laxiflora,* which is widespread in Mexico and Central America, is, I think, much more closely akin to numerous South American species of *Siphocampylus* than it is to the rest of the genus *Lobelia.* Because of its slit corolla-tube, however, it has been assigned without hesitation to *Lobelia* by most botanists. To transfer it to *Siphocampylus,* regardless of the possible theoretical value of such a course, would not only confuse the nomenclature but would necessitate the revision of the generic limits of *Siphocampylus* to an undue degree and would tend to break down the already somewhat nebulous distinction between it and *Lobelia.* An adequate revision of the generic characters of *Lobelia* and *Siphocampylus* is greatly to be desired.   The genera in question, while apparently good natural groups, have been so arbitrarily separated in the past that their truly definitive characters, if any, have been obscured.

When subjected to critical examination, the characters that separate *Laurentia* and *Isotoma* from the large genus *Lobelia* are seen to break down

[3] Studies on the flora of northern South America—IV. The genus *Burmeistera*. Bull. Torrey Club 52: 93–104. 1925.

entirely. The principal character, the presence or absence of a dorsal slit or cleft in the corolla-tube, is of no real value as an indicator of generic differences. Many species of *Lobelia*, closely related otherwise to North American species, have the cleft extending only part way to the base, usually three-fourths of the distance or more. The only species of *Lobelia* native to southern Europe, *L. urens*, has the tube cleft almost exactly halfway, while the little-known *L. sinaloae*, of western Mexico, lacks the cleft entirely. The last-mentioned species, is, therefore, a *Laurentia* by morphological standards, but is so closely related to *Lobelia Hartwegi* as to be scarcely distinguishable from that species except by the single feature of the corolla-tube.

The adherence of the filaments to the corolla-tube is also a variable feature throughout the Lobelioideae, varying roughly in accordance with the depth of the dorsal cleft of the corolla-tube. In general, the filaments are more likely to be adnate to the corolla in species having the corolla-tube without a dorsal cleft, but the degree of adherence is variable and no sharp line can be drawn between the species having free stamens and those with stamens adherent to the corolla.

It is proposed, therefore, to unite with the widespread genus *Lobelia* the two somewhat localized groups previously known as *Laurentia* and *Isotoma*. The latter is entirely Australian, and appears to differ from the former in no way except that in some species the three lower corolla-lobes are scarcely broader than the two upper ones, which makes the limb of the corolla appear almost regular. *Isotoma* was originally proposed by Robert Brown[4] as a section of *Lobelia*, and this section may now be taken to include the southern European, African and North American species described under *Laurentia* (except as mentioned below), and the Australian species described under *Isotoma* as a genus. Such a concept of generic limits will necessitate the formation of a very few if any new names, since most of the species concerned have already been given names in the genus *Lobelia*.

It seems to me that one cannot logically maintain genera which are widely distributed, the species of which differ from the species of other widespread genera by trivial and inconstant characters, so that the supposed genera have to be separated by purely mechanical analysis. If genera are actual phylogenetic units they will inevitably be small and homogeneous (and ordinarily not of wide geographical distribution), or large and relatively heterogeneous, usually widespread in space, with similar variants appearing in different parts of the range, the variants never wholly separable from each other nor from the original genus. The small and homogeneous genera just mentioned are mostly recognizable by some striking combination of characters, while such artificial genera as *Laurentia* are not definable except in the most arbitrary fashion.

    Prodr. Fl. Nov. Holl. 565. 1810.

Such definition of generic limits appears to be a natural consequence of organic evolution. A genus may be expected to be in the process of evolution, in which case we should expect it to be relatively small and poorly differentiated from related groups, or it may be well-established and widespread, fairly homogeneous and wholly distinct from all related groups.

In view of such reasoning either *Laurentia* or *Isotoma* may be thought of as a concept rather than as an actual assemblage of species. The European, African, Australian, and American members of either "genus" are not more closely related to each other than to species of the large group *Lobelia* and, accordingly, it seems best to consider them all as species of a single genus, but perhaps as belonging to local manifestations of that genus. The Lobelioideae as a whole are almost certainly an ancient group, but evolution in some parts of the subfamily appears still to be active. In the future such localized phases of large genera may be recognized as genera, but at present they appear to be insufficiently distinct to justify such a course.

There are in North America several very diverse species and species-groups which have been, in the past, arbitrarily assigned to the genus *Laurentia,* or to *Isotoma.* One of these species (*Laurentia* or *Isotoma longiflora*) seemingly has its closest relative in the Hawaiian genus *Brighamia,* and apparently should be taken as the type species of a monotypic genus. Secondly, a group of 5 or 6 closely related species in Mexico and Central America forms a natural genus very near to some Mexican species of *Lobelia.* This group appears distinct from other genera by several characters of habit, flower and fruit, and is typified by *Diastatea virgata* Scheidw. (*Lobelia ramosissima* Mart. & Gal.). Finally, a single species in the Rocky Mountain region, and a second species ranging from California to Baja California have been included in *Laurentia.* The former seems to be generically distinct (*Porterella carnosula* (H. & A.) Torr.) and the latter, if not generically distinct, may be assigned to *Lobelia* (*Palmerella debilis* A. Gray; *Laurentia debilis* McVaugh).

The following key will serve to set forth the characters of the genera just discussed:

1. Corolla pure white, salverform, the tube narrowly cylindric, 50–135 mm. long, the lobes subequal; pedicels each with a pair of filiform bracteoles, 2–4 mm. in length, at or near the base; ovary inferior or very nearly so, the apex inclosed by the free rim of the hypanthium; seeds conspicuously foveolate-reticulate .... 1. *Hippobroma*

1. Corolla blue or purplish, sometimes pale, strongly bilabiate, three of the lobes much broader than the other two; flower, including hypanthium, 25 mm. long or less; pedicels ebracteolate; seeds smooth, lustrous 2

    2. Ovary inferior or essentially so; corolla withering after anthesis, not enlarged in fruit. 3

        3. Corolla-tube 3.5–6.0 mm. long; plants wholly glabrous; foliage-leaves very nar-

rowly linear or rarely lanceolate, entire, rarely more than 2.0 mm. wide; flower-bracts mostly broader than the leaves; seeds fusiform, dark-apiculate.

4. *Porterella*

3. Corolla-tube 9.0–18.0 mm. long; plants bristly-pubescent above, at least on the corolla-tube; foliage-leaves broader, serrate, the middle and upper ones rarely less than 2.5 mm. wide, and the lower ones rarely less than 5.0 mm. wide; flower-bracts narrower than the leaves; seeds ellipsoid-lenticular, with rounded ends.

3. *Lobelia § Isotoma*

2. Ovary superior or attached to hypanthium at very base only; corolla much distended by the developing capsule and becoming at length scarious and hyaline.

2. *Diastatea*

1. HIPPOBROMA G. Don, Gen. Syst. **3**: 717. 1834.

Lobelia, sect. *Solenanthis* Kunth, HBK. Nov. Gen. & Sp. **3**: 309. 1819.
Isotoma, sect. *Solenanthis* A.DC., DC. Prodr. **7**: 412. 1839. TYPE SPECIES: *H. longiflora* Don, *l.c.*

Stems coarse, with acrid, milky, poisonous juice, erect or decumbent, to 7 mm. in diameter at base, simple or with a few subordinate side branches, pubescent at least above, or nearly glabrous, pale yellow-green, 15–50 (90) cm. high. Cauline leaves from few to 25, spreading or ascending, mem-branous, pubescent on the veins and on the lower surface or almost glabrous, said to be dull blue-green above and glossy gray-green beneath. Blades ellip-tic to oblanceolate, coarsely repand-dentate and minutely callose-denticulate on the margin, narrowed abruptly to the obtuse or acutish mucronulate apex and drawn out slowly to the narrow subpetiolar decurrent base. Size of blade 2.5–6.0 × 10–24 cm., usually 3–4 times as long as wide. Roots somewhat fleshy (woody?); perennial?

Flowers 8–35 in the axils of the upper leaves, the "inflorescence" 6–26 cm. long and comprising half to two-thirds the height of the entire plant or even more. Pedicels more or less upright in flower (declined in fruit), 7–15 mm. long in fruit, about 1 mm. in diameter, short-hirsute, each normally with a pair of filiform bracteoles, 2–4 mm. in length, at or near the base.

Hypanthium in anthesis turbinate, sparsely short-hirsute, becoming el-lipsoid or ellipsoid-campanulate in fruit, 7–9 mm. in diameter. Capsule ¾ inferior or more, often appearing wholly inferior because closely invested by the free rim of the hypanthium. Capsule pendent when mature, dehiscing loculicidally by two apical valves. Calyx-lobes narrowly linear, 1 mm. wide by 10–22 mm. long, callose-denticulate on the margins, ciliate or nearly glabrous.

Flower 80–160 mm. long, including hypanthium. Corolla salverform, pure white, slightly fragrant, puberulent except on the inner side of the lobes. Tube entire, narrowly cylindric, 50–135 mm. long, 1.0–2.5 mm. in diameter. Lobes subequal, spreading, 3–10 mm. wide by 13–27 mm. long. Filaments 58–95 mm. long, equalling or somewhat exceeding the corolla-tube, connate by their edges (or exceptionally free) at apex, adnate to the corolla-tube and free from each other from base to a point just below the apex of the tube. Anther-tube 5–6 mm. long by about 2 mm. in diameter, the orifice oblique and not closed by the three longer anthers; all anthers white-bearded at extreme tip, the two shorter ones densely tufted.

Seeds ellipsoid or cylindric with rounded ends, 0.6–0.8 mm. long, light brown, minutely and regularly foveolate-reticulate.

A single species, with characters of the genus:

1. HIPPOBROMA LONGIFLORA (L.) G. Don, Gen. Syst. **3**: 717. 1834. *Lobelia longiflora* L., Sp. Pl. 930. 1753; Type locality: "Habitat in Jamaica ad ripas." TYPE: Not seen. Linnaeus apparently had no specimen in 1753 and perhaps based his description merely upon Sloane's plate and description of 1707.[5] Rendle[6] states that there is extant a specimen in the Sloane herbarium at the British Museum. This should properly be regarded as the TYPE. *Rapuntium longiflorum* Mill., Dict. ed. 8. 1768. *Isotoma longiflora* Presl, Prodr. Mon. Lob. 42. 1836. *Laurentia longiflora* E. Wimm. in Macbr., Field Mus. Publ. Bot. **13**(6): 474. 1937, non Schlechter, 1922.

River-banks, clearings, fields and waste grounds. Widely distributed as an escape from cultivation in tropical and subtropical regions of both hemispheres. Throughout both Greater and Lesser Antilles. In continental North America extending from Florida (where collected by Rugel) along the Gulf Coast and southward throughout the lowland areas of Mexico and Central America, north on the west coast to Sonora. Rare at elevations of more than 1,000 meters. Flower and fruit throughout the year.

Although now rather widely distributed in the tropics as a weedy species, *Hippobroma longiflora* seems originally to have been confined to the West Indies. The evidence for this is twofold. In the first place, in a very large proportion of the situations where the species now occurs outside the West Indies, it is known to be an escape from cultivation, or is thought by the collector to be an introduced species. Its somewhat weedy nature and the habitats in which it is found tend to add weight to this evidence. In the second place, the species is seemingly becoming more frequent in various parts of tropical America. The early travellers do not mention it from continental America; Kunth[7] lists it from Cuba only; it is not mentioned in Seemann's *Flora of Panama*.[8] Alphonse De Candolle, in the *Prodromus*[9] says merely "in paludosis Caribaeorum." There are collections from Cuba and Puerto Rico in the herbarium of Sessé and Mociño (approximate date 1800), but the species is not mentioned in the *Plantae Novae Hispaniae*,[10] and apparently the collectors did not find it in their Mexican travels. Grisebach[11] says nothing of its occurrence in continental America, and, as late as 1887, Hemsley,[12] in the *Biologia Centrali-Americana*, knew but a single locality for the species on the continent of North America. The earliest con-

[5] A Voyage to the islands Madera . . . Jamaica, with the natural history, etc. **1**: 158. t. 101. f. 2. London, 1707.
[6] Fl. Jamaica **7**: 139. 1936.
[7] HBK. Nov. Gen. & Spec. **3**: 309. 1819.
[8] Flora of the Isthmus of Panama; in *The Botany of the Voyage of H.M.S. Herald*, pp. 57–254. 1854.
[9] Prodr. Syst. Nat. Regni Veg. **7**: 413. 1839.
[10] Plantae Novae Hispaniae. 1–184, i–xiii. Mexico, 1887.
[11] Flora of the British West Indian Islands. i–xvi, 1–789. London, 1864.
[12] Biologia Centrali-Americana **4**: 103. 1887.

tinental collections that I have seen are those of Rugel (1842 to 1849) from Florida, and of Schott (1864 and 1865) from Merida, Yucatan. It seems probable that the major portion of its spread in range has been in the last hundred years or less.

This plant was known to the early botanical explorers of the West Indies, and excited considerable interest because of its poisonous properties. It was described as *Lobelia longiflora* by Linnaeus and was subsequently transferred to *Isotoma* by Presl. Subsequent authors have followed Presl for the most part, but such a stand appears indefensible. *Isotoma*, as originally delimited, was a small Australian group, the species of which are scarcely separable generically from the African *Laurentia*. The transfer of the West Indian species to *Isotoma* was made because of the single character of the subequal corolla-lobes, a character that was emphasized in the original description of *Isotoma*. A glance at material of almost any of the Australian Isotomas, however, will make clear that the generic name is, in a sense, a misnomer; the lobelioid character of the corolla is plainly evident, with two small lobes opposed to three broader ones.

Linnaeus' *Lobelia longiflora* bears ample evidence of its relationship to the majority of endemic Lobelioideae of the West Indies. Its seeds bear close resemblance to those of many other species. The conspicuous free rim of the hypanthium simulates that found in many West Indian Lobelias, as do the bracteoles of the pedicel and the whole aspect of the calyx and capsule. The corolla, on the other hand, is unlike that of any other known species in America, but is closely similar to that of *Brighamia*, which is confined to the Hawaiian Islands.

The species is clearly marked, distinct from all other known species by the following combination of characters: Corolla white, salverform, the tube very long in proportion to its diameter, the lobes subequal; pedicels bracteolate; free rim of the calyx surpassing the ovary, which is nearly wholly inferior; seeds foveolate-reticulate. It appears reasonable to regard this as the only species of a distinct genus, quite apart from *"Laurentia," "Isotoma,"* and *Lobelia*. The earliest available name for such a genus appears to be that proposed by Don. According to Dalla Torre and Harms (Gen. Siph. 521. 1900–1907) this name is antedated by *Stooria* (Neck., Elem. 1: 131. 1790). Necker's genera are so poorly characterized, however, that it is impossible to determine their identities.

2. DIASTATEA Scheidweiler, Allg. Gartenz. 9: 396. 1841.

TYPE SPECIES: *Diastatea virgata* Scheidw., *l.c.*

Stems erect, simple or with from few to many ascending subordinate lateral branches from the basal half. Plants annual, with branched fibrous roots. Leaves cauline, membranaceous or chartaceous in dried material, the

upper and middle ones largest and acutely pointed, the lower ones decreasing in size downward and the lowest often obtuse or rounded.

Inflorescences racemose, terminal on the branches, the central one usually much exceeding the others, if any. Racemes simple, slightly to strongly secund, loosely flowered (flowers usually 1 cm. apart on the axis, or more than this). Pedicels filiform, spreading-ascending, often upcurved or bent distally so that the mature capsule is erect or nearly so, ebracteolate. Flower-bracts foliaceous, the lowest similar to the upper leaves in size and shape, the upper narrower, the uppermost linear.

Hypanthium in anthesis broadly cupshaped, varying to flattish or to obconic, glabrous or roughened at base, much exceeded by the ovary, in fruit nearly unchanged or becoming obconic or turbinate. Capsule superior or nearly so, inclosed by the stretched persistent corolla, not more than ⅓ of its length contained in the hypanthium (rarely nearly ½ its length in exceptional individuals of *D. tenera*), bilocular, dehiscing loculicidally by apical valves. Placentae axile.

Flower inverted in anthesis. Corolla glabrous, purplish-blue. Tube in anthesis narrowly cylindric (except in *D. expansa*), entire, not slit dorsally, the dorsal sinus about as deep as the lateral ones. Tube much stretched by the expanding capsule and becoming at length scarious and hyaline. "Upper" lobes (the two opposite the three larger anthers) oblanceolate or with an elliptic blade and a long claw, mostly with an expanded deltoid base. The three "lower" lobes fused into a distinct lip, this more or less abruptly deflexed and bituberculate at base.

Filaments equalling or slightly exceeding the corolla-tube, connate a part of their length above, below free from each other and loosely adherent to the corolla-tube. Anther-tube bluish gray, two of the anthers shorter than the others and minutely white-tufted at tip; three larger anthers mostly glabrous.

Seeds many, light-brown, ellipsoid, smooth and shining, 0.5–0.6 mm. in length.

There are in this genus six well-defined entities, of which three are here described as new. The genus is characterized by the almost superior ovary and capsule, and by the long-persistent corolla which is much distended by the developing ovary and becomes at length hyaline. The group as a whole is closely akin to some Mexican species of *Lobelia,* and is, indeed, separable from these by arbitrary characters only. *L. sublibera,* a montane species of Tamaulipas and Nuevo Leon, has capsule and corolla characters almost identical with those of the species of *Diastatea,* the one exception being the corolla-tube which in *L. sublibera* is slit nearly to the base. The same thing is found to a lesser extent in *Lobelia xalapensis,* a wide-spread species of tropical America; in this species the capsule is about one-third inferior, and the corolla is somewhat enlarged and persistent. *Lobelia Dielsiana,* a local but perfectly distinct species of southwestern Mexico, not only has the superior ovary and the corolla of *Diastatea,* but has the corolla-tube slit not more than two-thirds its length.

The earliest available name for such a genus appears to be *Diastatea*, proposed by Scheidweiler in 1841. The single species described, *D. virgata*, was said to grow in "Mejico." Scheidweiler's original material has not been located, but his description can apply to no species except the one subsequently described as *Lobelia ramosissima* Mart. & Gal. The descriptions of *Diastatea* and of *D. virgata* are reprinted below, with the critical or diagnostic phrases italicized:

"DIASTATEA *mihi. Calycis tubo subnullo*, limbo quinquepartito; corolla fauci calycis inserta, *tubo longissimo integro*, limbo bilabiato, laciniis superioribus angustioribus; stamina 5 cum corolla inserta, filamenta libera, glabra, antherae in tubum connatae, superiores dorso hispidae, inferiores biaristatae, aristae inaequales. *Ovarium sessile, liberum, cylindricum;* stylus et stigma Lobeliae; *capsula bilocularis, supera, libera, tubo corollae *inclusa*; semina indefinita.

"DIASTATEA *virgata.* Planta perennis ? ramosissima, ramis virgatis; *foliis inferioribus ovatis, superioribus lanceolatis, omnibus incisodentatis,* acutis, apice integerrimis, decurrentibus, caule ramulisque glabris; pedunculis axillaribus solitariis, filiformibus, *calycis laciniis subulatis utrinque margine uni-biglandulosis,* glandulis stipitatis; corollae limbi laciniis mucronulatis; flores coerulei."

Scheidweiler was so much impressed by the differences between his plant and the species of *Lobelia* known to him that he went on to emphasize the generic characters of *Diastatea* in German: " . . . der Fruchtknoten in der Mitte des Fruchtbodens ist ganz frei, ausser allem Zusammenhange mit dem Kelche; die Kapsel ist ebenfalls frei, und bleibt nach der Reife von der Kronenröhre umhüllt."

Diastatea as a whole appears to be somewhat more highly evolved than the genus *Lobelia.* The annual duration of all the species points to this, as do the characters of the nearly superior ovary, the ebracteolate pedicels, the peculiarly formed corolla, and the distribution, which is centered in Central America and southern Mexico.

<div align="center">KEY TO THE SPECIES</div>

1. Corolla-tube 4.0–4.5 mm. long, narrowest at base and much enlarged distally; filaments 4.0–4.5 mm. long; middle and upper leaves lanceolate or narrowly elliptic, 4–8 times as long as wide, 0.3–0.4 cm. wide .... 1. *D. expansa*

1. Corolla-tube (in anthesis, before swollen by the expanding capsule) linear, narrowly cylindric, not at all enlarged distally... 2

     2. Middle cauline leaves linear or narrowly elliptic, 0.1–0.25 cm. wide; filaments 6.0– 7.5 mm. long (rarely 5.0–9.0 mm.); calyx-lobes glabrous, entire or toothed, 1.0–3.5 mm. long .... 4. *D. tenera*

     2. Middle cauline leaves linear-lanceolate or broader, 0.3–4.0 cm. wide; if less than 1 cm. wide, the filaments 3.0–4.8 mm. long... 3

         3. Filaments 3.0–4.8 mm. long; flower, including hypanthium, 4.5–10.0 mm. long... 4

4. Calyx-lobes strongly prickly-ciliate on margins, 0.5–1.0 mm. wide at base, 4.0–6.0 mm. long; pedicel usually plainly scabrous under a lens; capsule 2.5–3.5 mm. in diameter; flower-bracts linear or nearly so, mostly strongly appressed to the stem. Pubescence mostly confined to the wing-like angles of the stem. .... 3. *D. costaricensis*

4. Calyx-lobes glabrous or sparingly ciliate, rarely as much as 0.5 mm. wide at base, 1.5–3.5 (rarely 5.5) mm. long; pedicel smooth and glabrous; capsule 1.5–2.5 mm. in diameter, flower bracts not appressed, the lower lanceolate or broader. Pubescence evenly distributed around the terete or angled stem.
  2. *D. micrantha*

3. Filaments 7.5–11.0 mm. long; flower, including hypanthium, 12–22 mm. long . 5
   5. Calyx-lobes entire but closely and prominently ciliate on margins; pedicels prickly-ciliate under a lens; stem terete or angled, not winged, pubescent below with evenly distributed soft hairs . ...5a. *D. virgata* var. *ciliata*

   5. Calyx-lobes glabrous but with minute teeth on margins; pedicels smooth and glabrous; stem winged from the decurrent leaf-bases, with stiffish hairs on the margins of wings and few if any elsewhere . . .. 5. *D. virgata*

1. **Diastatea expansa** McVaugh, sp. nov. Corollae tubo infundibuliforme, basi plus minusve gibboso, 4.0–4.5 mm. longo; filamentis 4.0–4.5 mm. longis; lobis calycis glabris, minute dentatis, 2.5–3.5 mm. longis; foliis mediis superioribusque ellipticis lanceolatisve, inferioribus latioribus.

Type locality: Correra, Dist. Temascaltepec, Estado de Mexico, at 1230 meters elevation. TYPE, *G. B. Hinton 2644*, Nov. 19, 1932, in the Gray Herbarium.

Stems simple or with a few weak side branches, slender (1 mm. in diameter at base), purplish below, 20–25 cm. high, glabrous, minutely scabrous on the somewhat winged angles. Leaves 8–14, thin, glabrous, spreading or somewhat appressed, the middle and upper ones elliptic or lanceolate, acute at tip, acute or rounded at base, sessile, 0.3–0.4 cm. wide by 1.3–2.5 cm. long, the margins finely and regularly serrate with 5–7 prominent teeth per cm. Lower leaves smaller and relatively broader, the lowest obtuse, suborbicular, subpetiolate, about 0.3 by 0.3 cm.

Inflorescence weakly secund, from few- to 11-flowered, few to 11 cm. long. Pedicels laxly ascending (in flower), to 11 mm. long in flower, smooth and glabrous. Flower-bracts leafy (except sometimes the uppermost), elliptic or lanceolate to linear, the lower ones 0.4–0.5 cm. wide by 1.8–2.5 cm. long.

Hypanthium glabrous, 1 mm. long or less. Ovary fusiform, 3 mm. long in anthesis. Fruit not seen. Calyx-lobes linear-lanceolate, acute, glabrous with 1 or 2 minute teeth on each edge, 2.5–3.5 mm. long.

Flower 8.5–9.5 mm. long, including hypanthium. Corolla purplish-blue (when dried). Tube 4.0–4.5 mm. long, slightly gibbous at base on lower side (in line with the two smaller anthers), narrowest at base and gradually expanded distally. Two upper lobes oblanceolate, 1.0–1.3 mm. wide by 4.0–5.0 mm. long; lobes of the lower lip elliptic, 2.0–2.5 mm. wide by 4.0 mm. long. Filaments 4.0–4.5 mm. long. Anther-tube 1.3–1.5 mm. long.
Seeds not seen.

Known only from the type collection.

2. **DIASTATEA MICRANTHA** (HBK.) McVaugh, Bull. Torrey Club **67**: 143. 1940.
  Lobelia micrantha HBK., Nov. Gen. & Sp. **3**: 316. 1819 (247 of folio ed.).

Type locality: Ecuador. ("in Regno Quitensi, prope pagum Puembo, alt. 1300 hex."). TYPE: not seen. ISOTYPE, in herb. Kunth, photographed in the herbarium of the Botanical Museum, Berlin (Field Mus. neg. 9110).

Lobelia subtilis HBK., *op. cit.* 317 (folio ed. 247), *ex char. Lobelia ruderalis* R. & S., Syst. **5**: 56. 1819, fide Kunth, HBK., *op. cit.* **3**: 455. 1820. *Lobelia Draba* R. & S., Syst. **5**: 67. 1819, fide Kunth, *l.c. Rapuntium micranthum* Presl, Prodr. Mon. Lob. 25. 1836. *Rapuntium subtile* Presl, *l.c. Lobelia parviflora* Mart. & Gal., Bull. Acad. Brux. **9**: 41. 1842 (TYPE, *Galeotti 1970,* from Oaxaca, seen in the herbarium of the Jardin Botanique de l'État, Bruxelles). *Lobelia minutiflora* Kunze, Linnaea **16**: 318. 1842, *ex char. Laurentia ovatifolia* B. L. Robinson, Proc. Amer. Acad. **26**: 166. 1891 (TYPE, *Pringle 2985,* from Jalisco, seen in the Gray Herbarium). *Dortmannia micrantha, D. minutiflora* O. Ktze. Rev. Gen. Pl. **2**: 972. 1891. *Dortmannia parviflora* O. Ktze., *op. cit.* 973. *Laurentia micrantha* A. Zahlbr., Bull. Torrey Club **24**: 386. 1897, non A.DC. *Laurentia pedunculata* Brandg., Univ. Calif. Publ. Bot. **6**: 73. 1914 (TYPE, *Purpus 6705* from Chiapas, not seen. ISOTYPES, in Gray Herbarium and herbarium of the New York Botanical Garden, are *D. micrantha*). *Laurentia Maximiliana* E. Wimm., Rep. Sp. Nov. **38**: 78. 1935, *ex char. Laurentia micrantha* var. *longibracteata* E. Wimm., Rev. Sudamer. Bot. **2**: 104. 1935. *Laurentia micrantha* var. *ovatifolia* E. Wimm., Field Mus. Publ. Bot. **13**(6): 476. 1937. *Laurentia michoacana* var. *ovatifolia* B. L. Robinson, Proc. Amer. Acad. **26**: 167. 1891, nomen nudum. *Laurentia michoacana* B. L. Robinson, *l.c.,* nomen nudum. *Lobelia Turckheimii* Vatke, ex B. L. Robinson, *l.c.,* nomen nudum.

Stem simple or with many ascending branches, very slender to somewhat coarse (maximum size about 3 mm. in diameter at base), green, or purplish below, or sometimes purple throughout, from few to 50 (75) cm. high, chaffy-pubescent, especially below, or varying to practically glabrous; hairs, when present, nearly uniformly distributed around the terete or angled stem, flaccid and collapsed when dried. Plants exceedingly variable in size and pubescence. Leaves mostly about 10 on the main stem, the middle and upper ones lanceolate to ovate, acute at tip, narrowed to a margined petiole or a distinct slender petiole as much as 0.7 cm. long, less often the blades sessile. Lower leaves smaller, ovate to orbicular, mostly obtuse and petiolate. Texture of blades chartaceous or membranaceous. Pubescence, when present, mostly concentrated near margin, on veins of lower surface, and on upper surface near base. Margin variously serrate, the principal serrations mostly sharp, 5–6 per cm., but the margin sometimes sinuate or coarsely jagged-toothed, or minutely serrulate with as many as 12 teeth per cm. Size of blades ranging up to 2.2 by 5.5 cm., these usually 1 to 2 times as long as broad. Petioles ranging from 0.3 to 1.3 cm. in length.

Inflorescences often somewhat secund, the principal one from few- to 25-(30-) flowered, from few to 25 (30) cm. in length. Pedicels 6–27 (42) mm. long in fruit, the distal end often upcurved in fruit, smooth and glabrous (less often ciliate or chaffy-hirsute). Lower flower-bracts lanceolate, resembling reduced leaves; upper bracts narrower, linear to filiform, toothed. Lower bracts 0.2–1.5 by 1.0–3.5 cm.; upper ones 0.3–1.5 cm. long.

Hypanthium mostly glabrous, in fruit becoming conic, slightly higher than broad, 0.5–1.0 mm. high. Capsule narrowly ellipsoid, 1.5–2.5 mm. in

diameter by 3.0–6.0 (8.0) mm. long (average size 2 by 5 mm.). Calyx-lobes linear, usually less than 0.5 mm. in width at base, acute to acuminate at tip, entire or ciliate-toothed, 1.5–3.5 (5.5) mm. long.

Flower 4.5–6.5 (8.0) mm. long, including hypanthium. Corolla dark purplish-blue to pale lilac, pale blue or white. Tube 2.5–4.0 mm. long. Two upper lobes broadly triangular, about 1.5 mm. long; lobes of the lower lip rounded-spatulate, about 1 mm. broad by 2.0 mm. long. Filament-tube (3.0) 3.5–4.0 (4.5) mm. long. Anther-tube (0.5) 0.7–1.1 (1.3) mm. long, the three larger anthers glabrous or somewhat pubescent.

Seeds about 0.5 mm. in length.

Well-drained situations; fields, pastures and roadsides, limestone ledges, thickets, pine forests, open hillsides and barrancas. Highlands of San Luis Potosí to Vera Cruz and Jalisco, south throughout the highlands of southern Mexico and Central America; in the Andes to Peru and Bolivia. Occurs mostly at elevations of 1,000 to 2,700 meters. Flower and fruit nearly throughout the year.

Diastatea micrantha is the most variable and the most widely distributed species of the genus. It ranges from San Luis Potosí to Bolivia and the many variations appear to be distributed throughout, without geographic segregation.

3. **Diastatea costaricensis** McVaugh, sp. nov. *D. micranthae* similis; marginibus loborum calycis valde echinato-ciliatis, lobis 4.0–6.0 mm. longis, basi 0.5–1.0 mm. latis, pedicellis sub lente scabris; capsulis diametro 2.5–3.5 mm.; bracteis sublinearibus, appressis; caulibus plus minusve alatis, alis ciliatis.

Type locality: near San José, Costa Rica. TYPE: *Oersted 9238*, November 1846, in the herbarium of the Universitetets Botaniske Museum, Copenhagen.

Laurentia irazuensis Wimmer in Standl., Field Mus. Publ. Bot. **18**(4): 1415. 1938, non *Lobelia irasuensis* Pl. & Oerst., 1857.

Stem simple or with few to many ascending branches, 0.5–2.0 mm. in diameter at base, usually purplish at least at base, few to 34 cm. high, usually somewhat wing-angled below the decurrent leaf-bases. Pubescence of subrigid chaffy hairs, mostly confined to the wing-angles of the stem, especially the basal portion; some of the hairs, at least the shortest ones, usually remaining erect and not collapsed in dried specimens. Leaves mostly about 10 on the main stem, papery, somewhat appressed, the middle and upper ones lanceolate to linear-lanceolate, acute or acuminate at tip, narrowed to a sessile cuneate base. Lower leaves smaller and relatively broader, acute or obtuse at tip, sessile or subpetiolate. Pubescence mostly confined to the margin, the veins of the lower surface, and the base of the blade on the upper surface. Margin finely but somewhat irregularly serrate with 4–8 teeth per cm. Blades 0.3–0.6 cm. wide by 1.0–2.5 cm. long; blades of lowest leaves as small as 0.2 by 0.3 cm.; upper and middle blades mostly 3–4.5 (6.0) times as long as wide.

Inflorescences usually plainly secund, the principal one 5–16 cm. in length, from few- to 13-flowered. Pedicels 4–16 mm. long in fruit, the distal end usually strongly upcurved in fruit, so that the capsule is erect, usually plainly scabrous under a lens. Flower-bracts narrowly elliptic to linear, the lower resembling reduced leaves, all appressed to the axis, usually strongly so; size (of lower bracts) 0.2–0.4 by 1.0–2.7 cm.

Hypanthium glabrous, in fruit about as broad as high, 0.8–1.1 mm. high. Capsule broadly ellipsoid, 2.5–3.0 mm. in diameter by 5.0–6.5 mm. long. Calyx-lobes narrowly triangular, usually plainly tapering from base to apex, 0.5–1.0 mm. wide at base, strongly prickly-ciliate on margins, 4.0–6.0 mm. long.

Flower 5.0–7.0 mm. long, including hypanthium. Corolla blue-purple. Tube 3.0–4.0 mm. long. Two upper lobes broadly triangular, 1.3–1.5 mm. long; lobes of the lower lip rounded-spatulate, about 1 mm. broad by 1.5 mm. long. Filaments 3.5–4.0 mm. long. Anther-tube 0.9–1.1 mm. long, the three larger anthers minutely pubescent.

Seeds about 0.5 mm. in length.

Grassy hillsides, pastures, roadside ditches. Guatemala to Costa Rica, at elevations of 800 to 1,800 meters. Flowering and fruiting from November to February (according to specimens seen).

Specimens examined:[13] GUATEMALA: without locality, *E. T. Heyde 381* and *537* (US); SANTA ROSA: Estanzuela, *Heyde & Lux, J. D. Sm. Pl. Guat. 4257* (G, NB, US); "in collib. herbid., Guatemala, Cerro del Carmen," *Bernouilli 146* (NB). COSTA RICA: Bords du Rio Torres près de San Francisco de Guadalupe, *Tonduz 7230* (US); San José, etc., *Tonduz 1414* (US); San Sebastian, Prov. San José, *Standley 32717* (US); Santa Marta de Dota, Prov. San José, *Standley 41587* (F); San Ramon, *A. M. Brenes 3777, 4752, 5300, 5860a, 16851* (F); prope San José, *Oersted 9238*, Nov. 1846 (Cop); Segovia, *Oersted 9244*, Jan. 1848 (Cop). HONDURAS—COMAYAGUA: vicinity of Siguatepeque, *Standley 55995* (F, US).

This species was first collected by Oersted in Costa Rica in 1846. It was later described by Planchon and Oersted under *Lobelia parviflora* "As far as one can judge from the short diagnosis of *Lobelia parviflora*, our material belongs to that species. It grows in meadows at San José, Costa Rica (4,000 ft. alt.), and at the same height in Segovia at Xinoteca; with flower and fruit in December and January." Wimmer later mistakenly identified the Oersted material of *Diastatea costaricensis* as *Lobelia irasuensis* Pl. & Oerst., which is a true *Lobelia* and not even closely related to the present species; the original description of *L. irasuensis* is carefully drawn, and the type, *Oersted 9246*, collected at 8,000 feet on Mt. Irazu, is preserved in the herbarium of the Universitetets Botaniske Museum, Copenhagen.

When *Diastatea costaricensis* grows in and about the same localities where *D. micrantha* is found, it is always easily separable from it. No true

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[13] See list of abbreviations for herbaria at end of paper.

intermediates have been seen, although occasional specimens show intergradation in one or two characters.

4. DIASTATEA TENERA (A. Gray) McVaugh, Bull. Torrey Club **67**: 143. 1940.

Palmerella tenera A. Gray, Proc. Amer. Acad. **22**: 433. 1887. Type locality: Rio Blanco, Jalisco. TYPE: *E. Palmer 552*, Sept. 1886, in the Gray Herbarium. *Lobelia Palmeri* Greene, Pittonia **1**: 297. 1889. *Laurentia pinetorum* Brandg., Univ. Cal. Publ. Bot. **4**: 92. 1910. TYPE, *Purpus 3665*, from Popocatapetl, not seen. ISOTYPES, in Field Museum, Gray Herbarium and New York Botanical Garden, are *D. tenera*.

Stem simple or with few subordinate side branches from the lower part, slender, usually not exceeding 1 mm. in diameter at base, purplish at least below, from few to 30 (64) cm. high, glabrous or minutely scabrous-puberulent, scabrous below on the angles. Leaves usually 6–8, thin, glabrous, somewhat appressed, the middle and upper ones linear or narrowly elliptic, acute at both ends, sessile, 0.1–0.25 cm. wide by 0.8–3.5 cm. long, the margins finely and shallowly serrulate with about 4 teeth per cm. Lower leaves smaller and relatively broader, obtuse or acute, mostly 0.2–0.4 cm. wide by 0.3–0.8 cm. long, sessile, or less often subpetiolate.

Inflorescence usually strongly secund, from few to 15 (32) cm. long, loosely from 1- to 10- (20-) flowered. Pedicels usually arcuate (sometimes abruptly upcurved near tip) so that the mature capsule is erect or nearly so, often somewhat thickened beneath the hypanthium and merging imperceptibly with it, 6.0–20.0 (48.0) mm. long, smooth and glabrous. Flower-bracts (except occasionally the lowest) linear, resembling reduced leaves, 1.0–2.0 mm. wide by 5.0–15.0 (20.0) mm. long.

Hypanthium usually oblique, glabrous, becoming conic or turbinate in fruit, as long as or longer than broad, 1.0–1.5 (3.0) mm. high. Capsule 1.5–2.5 (3.5) mm. in diameter by 5.0–7.0 (8.0) mm. long. Calyx-lobes linear to elliptic or lanceolate, acute at tip, glabrous, with 1 or 2 minute teeth on each edge or less often entire, (1.0) 1.5–3.0 (3.5) mm. long.

Flower 10–16 mm. long, including hypanthium. Corolla purplish-blue ("purple," or "deep lilac"), with white or yellowish eye, the lower lip bituberculate at base. Tube narrowly cylindrical, not expanded above, (the lobes flaring abruptly) slightly gibbous at base on lower side, (in line with the two shorter anthers) 5.0–7.5 (8.0) mm. long. Two upper lobes linear-spatulate, 1.0–1.5 mm. wide by 3.5–5.0 mm. long; lobes of the lower lip obovate, rounded or truncate at tip, mucronate, 1.5–2.5 (4.0) mm. wide by 4.0–7.0 mm. long. Filaments (5.0) 6.0–7.5 (9.0) mm. long. Anther-tube (0.8) 1.0–1.3 (1.5) mm. long, the three larger anthers minutely puberulent or glabrous.

Seeds about 0.5 mm. in length.

Pine forests, streamsides, damp grassy glades, barrancas, moist meadows and mountainsides, at elevations of 1,400 to 2,600 meters. Jalisco to Puebla and Guerrero.

Specimens examined: MEXICO—GUERRERO: Petlacala, *Mexia 8959* (USNA). JALISCO: Sierra de San Esteban, *Pringle 8756* (ANS, F, G, NB,

US); near Guadalajara, *Rose & Painter 7474* (G, US); near Guadalajara, *Pringle 2374* (ANS, G, NB), *Pringle 2163* (F, G); Rio Blanco, *Dr. Edw. Palmer 552* (ANS, G, TYPE; NB); San Sebastian, e. of Arroyo del Cura, *Mexia 1378* (NB, US); Road to San Domingo Mine, Etzatlan, *Barnes & Land 319* (F). MEXICO (Estado de): Tultenango, *Pringle 3527* (G); near Tultenango, *Rose & Painter 7842* (G, US); Dist. Temascaltepec, Carboneras, *Hinton 2122* (NB), Volcan, *Hinton 2507* (NB), *Hinton 2211* (NB), Communidad, *Hinton 2457* (G). MICHOACAN: Cerros San Miguel, *Bro. G. Arsene 6070* (NB, US), *6064* (NB, US), *5565, 6539, 6542* (US); La Huerta, *Bro. G. Arsene 5979* (US); Loma Santa Maria, *Bro. G. Arsene 3113* (US), *5865* (G, US). MORELOS: near Cuernavaca, *Pringle 7058* (G); mountainside above Cuernavaca, *Pringle 15028* (G). PUEBLA: Tepoxuchil, near Puebla, *Bro. Nicolas* (G, US); Manzanilla, *Bro. G. Arsene 2373* (US); Laguna de San Baltasar, *Bro. G. Arsene 57* (US); pres l'Hacienda Alamos, route de Veracruz, *Arsene 7073* (US); Fort la Guadalupe, *Arsene 269* (US); STATE UNKNOWN: Popocatepetl, *C. A. Purpus 3665* (F, G, NB).

D. tenera is more variable in flower-size than is usual in this genus, but all the material seen appears to be sufficiently uniform in character to justify its inclusion in a single species.

5. DIASTATEA VIRGATA Scheidw., Allg. Gartenz. 9: 396. 1841. Type locality: Mexico. TYPE: not seen.
   Lobelia ramosissima Mart. & Gal., Bull. Acad. Brux. 9: 42. 1842. Type locality "cordillere orientale d'Oaxaca." TYPE: *Galeotti 1971*, in the herbarium of the Jardin Botanique de l'État, Bruxelles. *Laurentia ramosissima* Benth. & Hook. f., ex Hemsley in Biol. Cent. Am. Bot. 2: 265. 1881.

Stems simple or with few to many branches, sometimes with much-branched bushy habit; branches strongly ascending. Stems green or purplish at base, sometimes more than 2.5 mm. in diameter at base, from 15 to more than 45 cm. high, conspicuously winged from the decurrent leaf bases, the wings chaffy-pubescent with stiffish hairs, especially on the lower parts of the stem. Leaves thin and papery, glabrous or sparsely hispid near the base and on margin, from few to 10, spreading, coarsely incised-dentate; size (of leaves at base of inflorescence) 1.3 × 4.3 cm.; middle cauline leaves 1.5–2.5 cm. broad by 2.5–6.0 cm. long; shape elliptic to lance-ovate (lower "ovate-subrhomboid" according to Mart. & Gal.), or the upper ones narrowly lanceolate to linear, merging into the flower-bracts. Tip blunt-pointed, mucronulate. Base cuneate, sessile or subpetiolate, or the lowest leaves with a petiole to 0.8 cm. long, and the base rounded.

Inflorescence secund, 15–30 cm. long, loosely from 10- to 25-flowered. Pedicels smooth, often arcuate, strongly ascending or the lowest widely spreading, 12–30 (55) mm. long in fruit. Flower-bracts linear or the lower broader, leafy; middle and upper ones usually about 1.0 cm. long.

Hypanthium in anthesis about 1 mm. long, glabrous, in fruit about the same size. Capsule 2.0–2.5 mm. in diameter by 9.0–13.0 mm. long, elliptic to linear, often slightly curved. Calyx-lobes narrowly linear, acutely pointed, 2.5–6.5 mm. long, minutely callose-denticulate on margins.

Flower 17–22 mm. long, including hypanthium. Corolla "bleu," the tube 8–11 mm. long, in anthesis narrowly linear, about 1 mm. in diameter. Lobes

of the lower lip spreading, deflexed, obovate or elliptic, 2.5–3.5 mm. broad by 6.0–8.5 mm. long. Two upper lobes linear to elliptic-oblanceolate, usually clawed, 1.5–2.0 mm. wide by 4.0–6.0 mm. long. Filament-tube 8.0–11.0 mm. long, the filaments shortly connate above. Anther-tube 1.6–2.0 mm. long.
Seeds about 0.6 mm. in length.

Mountains of Oaxaca and (?) Vera Cruz, at elevations of 1,000 to 2,000 meters. Collected in flower and fruit from November to February.

Specimens examined: MEXICO—OAXACA: Yavezia, *Galeotti 1971* (Brux, TYPE; US); Jayacatlan, *L. C. Smith 284* (G); Monte Alban, near Oaxaca City, *Chas. L. Smith 721* (NB, US); El Parian, Etla, *Conzatti & Gonzalez 904* (G); La Hoya Canyon, *Pringle 5887* (G); Santa Catarina, *Conzatti 1665* (F). VERA CRUZ: "Cordillera, Vera Cruz," 3,000 ft., *H. Galeotti*, fevrier (1840?) (US).

5a. DIASTATEA VIRGATA Scheidw., var. **ciliata** McVaugh, var. nov. *D. virgatae* similis; lobis calycis integris, valde ciliatis; caulibus teretibus vel angulatis, non alatis, ubique pubescentibus; pedicellis sub lente scabris; foliis mediis late ovatis, acute serratis, non incisis.

Type locality: Mountains above Iguala, Guerrero. TYPE: *Pringle 8375*, in the Gray Herbarium.

Habit essentially that of *D. virgata*. Stem terete or angled, not winged, chaffy-pubescent, especially below, with soft hairs which are more or less evenly distributed. Height 12–52 cm. Leaves thin and papery, about 10, sparsely pubescent on the veins below and on the upper surface and margin. Middle and upper leaves broadly ovate, acute at tip, rounded at base and narrowed abruptly into a margined petiole 1.0–5.0 mm. long, the blades 2.0–4.0 cm. wide by 2.5–6.0 cm. long. Margins irregularly and usually sharply serrate with 4–8 teeth per cm. Lower leaves smaller, the lowest often rounded and obtuse, petiolate.

Inflorescence secund, 9–17 cm. long, loosely from 10- to 16-flowered. Pedicels usually abruptly upcurved distally in fruit, 10–15 mm. long, rough-ciliate. Lower flower bracts leafy, usually ovate, the upper lanceolate to linear.

Hypanthium roughened at base, little changed in fruit, becoming 1.0–1.2 mm. high. Capsule ellipsoid, 2.0–2.5 mm. in diameter by 8.0–11.0 mm. long. Calyx-lobes linear or very narrowly triangular, long-pointed, entire but closely and prominently ciliate on the margins, 4.5–6.5 mm. long.

Flower essentially as in *D. virgata*. Length 12–14 mm., including hypanthium. Corolla purplish-blue (when dried). Tube 7.0–8.5 mm. long. Two upper lobes 1.0–1.5 mm. broad by 3.0–4.0 mm. long; lobes of the lower lip 1.5–3.0 mm. broad by 3.5–5.0 mm. long. Filaments 7.5–8.5 mm. long. Anther-tube 1.2–2.0 mm. long.
Seeds as in *D. virgata*.

Limestone hills and ledges, mountains of southern Mexico at altitudes of 900 to 1,200 meters. Flower and fruit from September to November.

Specimens examined: MEXICO—GUERRERO: mountains above Iguala, *Pringle 8375* (ANS, F, G, TYPE; NB, P, R, US). MEXICO: Vigas, Dist.

Temascaltepec, *Hinton 2628* (G). MICHOACAN: Cerro Azul, Morelia, *Bro. Arsene*, Sept. 17, 1910 (F). MORELOS: near Yautepec, *Pringle 11005* (F, G, NB, US).

This variety is very similar to *D. virgata,* to which specimens of it have previously been referred. The two are easily separated, however, by the key-characters noted above, as well as by the leaves, which in *D. virgata* are narrower and more prominently toothed than in var. *ciliata.* Geographically, also, the two appear to be distinct, although relatively few collections have been made of either.

3. LOBELIA, section *Isotoma* R. Br., Prodr. Fl. Nov. Holl. 565. 1810.

Laurentia Micheli, Nov. Pl. Gen. 18. t. 14. 1729; Adanson, Fam. Pl. **2**: 134. 1763. *Isotoma* Lindl., Bot. Reg. 964. 1826. *Palmerella* A. Gray, Proc. Amer. Acad. **11**: 80. 1876.

Ours perennial herbs with sessile leaves. Inflorescence a simple terminal raceme. Hypanthium in anthesis campanulate, the ovary inferior or essentially so. Placentation axile. Capsule bilocular, opening by apical loculicidal valves. Flower inverted in anthesis. Corolla strongly zygomorphic, the two (apparently) upper lobes narrower than the three lower ones, which are fused at base into a definite lip. Corolla-tube entire at apex, not cleft more deeply on the (apparently) upper side than between the upper and lower lips. Filaments united into a tube, at least distally. Anthers united into a tube, the two shorter ones white-tufted at apex and usually with short horn-like processes in addition. Seeds smooth, numerous.

A single species in North America, *Lobelia Dunnii* Greene.

KEY TO THE VARIETIES

1. Middle and upper leaves elliptic or lanceolate, 7.0–20.0 mm. wide; lower leaves obovate to oblanceolate, 9.0–30.0 mm. wide; plants usually bristly-pubescent at least in the inflorescence or, if glabrous, at least the corolla-tube pubescent 1a. *L. Dunnii* var. *serrata*

1. Middle and upper leaves linear or narrowly elliptic, 2.5–9.0 mm. wide; lower leaves oblanceolate, 5–12 mm. wide; plants usually entirely glabrous or sparsely bristly. ....1. *L. Dunnii* var. *Dunnii*

1. LOBELIA DUNNII Greene, var. **Dunnii** McVaugh, nom. nov. ·

Lobelia Dunnii Greene, Pittonia **1**: 297. 1889. Based on *Palmerella debilis. Palmerella debilis* A. Gray, Proc. Amer. Acad. **11**: 80. 1876. Type locality: "Great Canyon of the Tantillas Mts., near the northern borders of Lower California." TYPE: *E. Palmer*, in 1875, in the Gray Herbarium. *Laurentia debilis* McVaugh, Bull. Torrey Club **67**: 144. 1940, non *Lobelia debilis* L. f., 1781.

This variety differs from the more widespread var. *serrata* as follows:

Pubescence none, or sparse and confined to the inflorescence (corolla always pubescent). Cauline leaves narrower than in var. *serrata,* the middle and upper ones linear or narrowly elliptic, 0.25–0.9 cm. wide by 4.5–11.0 cm. long, mostly 10–20 times as long as wide; lower leaves oblanceolate, 0.5–1.2 cm. wide by 2.0–5.0 cm. long, mostly 3–6 times as long as wide. Serration

often inconspicuous except on the lowest leaves, the middle and upper ones with essentially entire margins lined with minute callose teeth.

Pedicels 4–9 mm. long, smooth and glabrous (rarely somewhat prickly). Bracts as in var. *serrata* but narrower, in proportion to the leaves. Hypanthium usually glabrous; calyx-lobes glabrous or nearly so, 5–8 mm. long.

Flower 22–30 mm. long, including hypanthium. Corolla-tube 12–18 mm. long. Filaments 12–17 mm. long. Anther-tube 2.0–2.5 mm. long, glabrous or with a few hairs, the two shorter anthers tufted as in var. *serrata*.

Habitat of var. *serrata;* also "dry hillsides" and "moist meadows"; mountains of Baja California, at elevations up to 2,200 meters. Collected in flower and fruit from August 1 to October 1.

Specimens examined: MEXICO—BAJA CALIFORNIA: "Tantillas Canyon, S. Diego Co.," *Edw. Palmer,* anno 1875 (G, TYPE); "Big Canyon, Tantillas Mts., s. part of San Diego Co.," *Edw. Palmer 210,* anno 1875 (F, NB); Big Canyon, *Geo. W. Dunn,* Sept. 20, 1881 (Cath, NB); Rancho San José, foot of Sierra San Pedro Martir, east of San Telmo, *Wiggins & Demaree 4814* (F, G, NB, P, US); Canyon Cantiles, *C. R. Orcutt,* Aug. 1, 1883 (F, G, US); La Sanca, Sierra San Pedro Martir, *Wiggins & Demaree 4861* (G, NB, P); La Encantada, Sierra San Pedro Martir, *Wiggins & Demaree 4996* (F, G, NB, P).

The nomenclatorial type of this species is a plant which has as yet not been found except in Baja California, where it was first collected by Dr. Edward Palmer in 1875. The far better-known variety *serrata* was discovered in California the same year.

1a. LOBELIA DUNNII Greene, var. **serrata** (A. Gray) McVaugh, comb. nov. *Palmerella debilis* var. *serrata* A. Gray, Bot. Calif. 1: 619. 1876. Type locality: "Valley of Ojai Creek, Ventura Co." (California). TYPE: *Rothrock 173,* in the Gray Herbarium. Isotypes seen in various herbaria. *Lobelia Rothrockii* Greene, Pittonia 1: 297. 1889. *Laurentia debilis* var. *serrata* McVaugh, Bull. Torrey Club 67: 144. 1940.

Stem decumbent or erect, simple or with ascending subordinate lateral branches, rather coarse (maximum size about 4 mm. in diameter at base), light green (often straw-colored below in dried specimens), 20–85 cm. high, smooth and glabrous below the inflorescence or sometimes throughout. Cauline leaves 20–35, spreading, membranous, at least the middle and lower ones smooth and glabrous, the upper ones glabrous to short prickly-pubescent. Middle and upper leaves elliptic or lanceolate, acute at both ends, sessile, 0.7–1.5 (2.0) cm. wide by 3.5–9.5 cm. long, mostly 5–10 times as long as wide. Lower leaves shorter and broader, obovate to oblanceolate, acute at tip, narrowed at base into a broadly margined petiole, (0.9) 1.5–2.5 (3.0) cm. wide by 3.5–6.0 (9.0) cm. long, usually 2–4 times as long as wide. All leaves serrate, the lower coarsely so with sharp teeth, the upper shallowly so, with callose narrow teeth. Plants perennial.

Inflorescence often subcapitate, 2–7 (12) cm. long, densely few- to 23-flowered. Pedicels strongly ascending or the lower spreading, rather stout (to 0.6 mm. in diameter in fruit), (2.0) 4.0–8.0 (13.0) mm. long in fruit,

short bristly-pubescent to glabrous. Flower-bracts linear or the lower lanceo-late or elliptic, resembling the upper leaves. Lower bracts attaining a size of 0.7 by 5.0 cm., but mostly about half this size; upper bracts linear, 2.0 cm. long or less.

Hypanthium in anthesis campanulate, mostly acute at base, bristly-pubescent to glabrous, campanulate to elliptic in fruit, 2.5–3.0 mm. in diameter. Capsule inferior or nearly so, 6–7 (12) mm. long. Calyx-lobes linear-subulate, with a short-deltoid base, entire, bristly-pubescent to glabrous, 6–14 mm. long.

Flower 20–25 mm. long, including hypanthium. Corolla-limb blue, the tube whitish (according to Jepson); both tube and limb pubescent, the former closely so within and less densely so without. Tube linear or nearly so, 9–12 (14) mm. long, at first entire, in age splitting incompletely on the dorsal side, split extending from near the base about half the length of the tube and exposing the dorsal filament. Lobes abruptly spreading from the summit of the tube, the two upper ones linear, acute, about 1 mm. wide by 5–7 mm. long; lobes of the lower lip fused at base, elliptic, 2.0–3.0 mm. wide by 6.0–8.0 (10.0) mm. long. Filaments 9.5–12.5 (14.0) mm. long, coherent into a tube above, free below nearly their whole length and loosely adherent to the corolla-tube, pubescent. Anther-tube 2.3–3.0 mm. long, bluish-gray, pilose with long white hairs, the two shorter anthers white-tufted at tip and sometimes with short straight hornlike processes in addition.

Seeds ellipsoid-lenticular, smooth and shining, light-brown, about 0.5 mm. in length.

Canyons and stream-beds, usually in moist soil, southern Coast-Ranges of California, from Monterey County to northern San Diego County and inland to the San Bernardino Mountains. Mountains, at elevations of 150 to 1,800 meters. Beginning to flower in June or early July; fruit August 1 to mid-October.

4. PORTERELLA Torrey, Hayd. Rep. Geol. Surv. Mont. 488. 1872.

Stems erect, simple or with few lateral branches, rarely diffuse and bushy, somewhat fleshy, very slender or stoutish, the maximum diameter at base about 4 mm. Color green. Entire plant smooth and glabrous, from few to 32 cm. high; plants occasionally with mature fruit when no more than 1.5 cm. high. Cauline leaves from few to 20, soft and lax, soon deciduous and often not persistent until flowering time, usually narrower than the flower-bracts. Blades sessile, entire or rarely sinuate in luxuriant specimens, linear-subulate or rarely lanceolate, 1.0–2.0 (4.0) mm. wide, (4.0) 10.0–20.0 (30.0) mm. long, the tip acute to acuminate or almost capillary. Plants annual, with slender fibrous roots; stem, in wet places, continued downward as an erect rootstock with roots at several nodes, plainly corky-parenchymatous below.

Inflorescence 6–20 cm. long (correspondingly less in dwarfed plants), loosely from 1- to 15- (25-) flowered. Pedicels spreading-ascending, slender (maximum diameter about 0.5 mm.), 5–20 (35) mm. long in fruit, expanded gradually into the base of the capsule, straight or arcuate. Flower-bracts linear to ovate, similar to the foliage leaves but usually broader and often longer than these, 1–4 mm. wide by 4–18 (27) mm. long, mostly 2.5–6.0 times as long as wide.

Hypanthium in anthesis narrowly obconic or turbinate, in fruit becoming turbinate or cylindric, long-acute and usually slightly oblique at base, (1.5) 2.0–3.0 mm. in diameter. Ovary inferior or essentially so. Placentation axile. Capsule bilocular, opening by apical loculicidal valves, (5.0) 7.0–10.0 (16.0) mm. long, wholly inferior or with 1–2 mm. of the tip not adherent to the hypanthium. Flower inverted in anthesis. Calyx-lobes linear, varying to narrowly triangular or elliptic, entire, rounded or acutish at tip, about 1.0 mm. wide (rarely as much as 2.5 mm.), 3–8 (11.0) mm. long.

Flower (9.0) 13.0–18.0 (20.0) mm. long, including hypanthium; odor said to resemble that of the cultivated heliotrope; corolla blue (rarely all white), with yellow or whitish eye and two folds at base of lower lip. Tube entire, linear or slightly enlarged distally, its long axis slightly oblique to that of the hypanthium, (3.5) 4.5–6.0 mm. long. Corolla strongly zygomorphic; two upper lobes erect, elliptic, 1.0–2.5 mm. wide, 3.5–5.5 mm. long; lobes of the lower lip elliptic or obovate, apiculate, 2–6 mm. wide, 4.5–9.0 mm. long. Filaments 3.0–6.0 (7.0) mm. long, coherent their whole length into a tube, free from the corolla. Anther-tube 1.5–2.6 mm. long, gray, all five anthers minutely white-tufted at tip, the two shorter ones plainly so, and with short horn-like processes in addition.

Seeds fusiform, light brown with minutely dark-apiculate tips, smooth and slightly lustrous, about 1 mm. long.

Marshes and wet meadows, margins of ponds, open muddy pools and ditches, growing in wet soil, often partially immersed; plants in partially dried mud are often dwarfed. Northwestern Wyoming to southeastern Oregon, south in the mountains to northern Utah, Coconino Co., Arizona, Elko Co., Nevada, and Tulare Co., California. Occurs principally at elevations of 1,500 to 3,000 meters. Flower and fruit mostly from June 15 to September 15.

A single species, with characters of the genus.

1. PORTERELLA CARNOSULA (Hook. & Arn.) Torr., *l.c.* (*P. carnulosa* Torr., *sphalm.*)

Lobelia carnosula Hook. & Arn., Bot. Beech. Voy. 362. 1840. Type locality: "Blackfoot River, Snake Country" (now southeastern Idaho). TYPE: Collected "by a friend of Mr. Tolmie" in 1837 and labelled "Tolmie"; now in the New York Botanical Garden. Sir J. Arthur Hill, who kindly instituted a search for the type of *Lobelia carnosula*, states that it is not to be found in the herbarium at Kew; the Tolmie plant at New York may therefore stand as the TYPE.

Laurentia carnosula Benth. & Hook. f., ex A. Gray, Bot. Calif. **1**: 444. 1876. *Porterella eximia* A. Nels., Bull. Torrey Club **27**: 270. 1900. Type locality: "Jackson's Lake, Uinta Co., Wyo." TYPE: *A. & E. Nelson 6544*, accession no. 20748 of the Rocky Mountain Herbarium of the University of Wyoming. *Laurentia eximia* A. Nels., New Man. Bot. Centr. Rocky Mts. 475. 1909.

In conclusion, the writer wishes to acknowledge his indebtedness to the curators of the several herbaria who have so kindly placed at his disposal

the collections in their charge. In citing exsiccatae, the following abbreviations are employed for herbaria:

ANS   Academy of Natural Sciences, Philadelphia, Pa.
Brux   Jardin Botanique de L'État, Bruxelles, Belgium.
Cath   Catholic .University of America, Washington, D. C.
Cop   Universitetets Botaniske Museum, Copenhagen, Denmark.
F   Field Museum of Natural History, Chicago, Ill.
FS   Forest Service, U. S. Dept. of Agriculture, Washington, D. C.
G   Gray Herbarium of Harvard University, Cambridge, Mass.
Id   University of Idaho, Pocatello, Ida.
NB   New York Botanical Garden, New York, N. Y.
O   National Herbarium of Canada, Ottawa, Ont.
Ore   University of Oregon, Eugene, Ore.
P   Pomona College, Claremont, Calif.
R   Rocky Mountain Herbarium, Univ. of Wyoming, Laramie, Wyo.
US   United States National Herbarium, Washington, D. C.
USNA   United States National Arboretum, Washington, D. C.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION
    BUREAU OF PLANT INDUSTRY
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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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New genera, species, and combinations are in **bold face** type. Capitalization of specific and varietal epithets approximates the recommendations of the International Rules of Nomenclature.

ERRATA

p.   1, l.   1, for "de Wildeman" read "De Wildeman."
      1, l. 14, for "similarily" read "similarly."
p. 83, l. 13, for "**Hammer**" read "**Hamner.**"
p. 86, l. 11, 13, 16, for "**Moxon**" read "**Maxon.**"
p. 169, l. 27, for "*Pottiae*" read "*Pottia.*"
p. 239, l. 22, delete the reference to "**C(arter)**"
      l. 24, for "pyrenomycestes" read "Pyrenomycetes," and before "Hill" insert "Tile."
p. 240, l. 10, for "Monographc du genre *Cistes*" read "Monographie du genre *Cistus.*"
p. 241, l. 24, for "indolelacetic" read "indolylacetic."
p. 245, l. 42, for "*Helianthemun*" read "*Helianthemum.*"
p. 246, l. 38, for "*Paeania*" read "*Paeonia.*"
p. 248, l. 18, for "*Fuscarium*" read "*Fusarium.*"
p. 367, Table 3, Transpose "orthodox" and "unorthodox."
p. 380, l. 5, omit comma after "here."
p. 412, l. 17, for "**Heinreicher**" read "**Heinricher.**"
p. 427, l. 14, for "*Preusii*" read "*Preussii.*"
p. 585, l. 23, for "*linarifolius*" read "*linariifolius.*"
      l. 24, for "*rotunifolia*" read "*rotundifolia.*"
p. 589, l. 10, for "*Goodyeria*" read "*Goodyera.*"
      l. 12, for "*cryptolepsis*" read "*cryptolepis.*"